THE GAMETOPHYTE OF *ACROSTICHUM SPECIOSUM* WILLD.

ALMA G. STOKEY & LENETTE R. ATKINSON
Mount Holyoke College, South Hadley, Mass., U.S.A. &
Amherst, Mass., U.S.A.

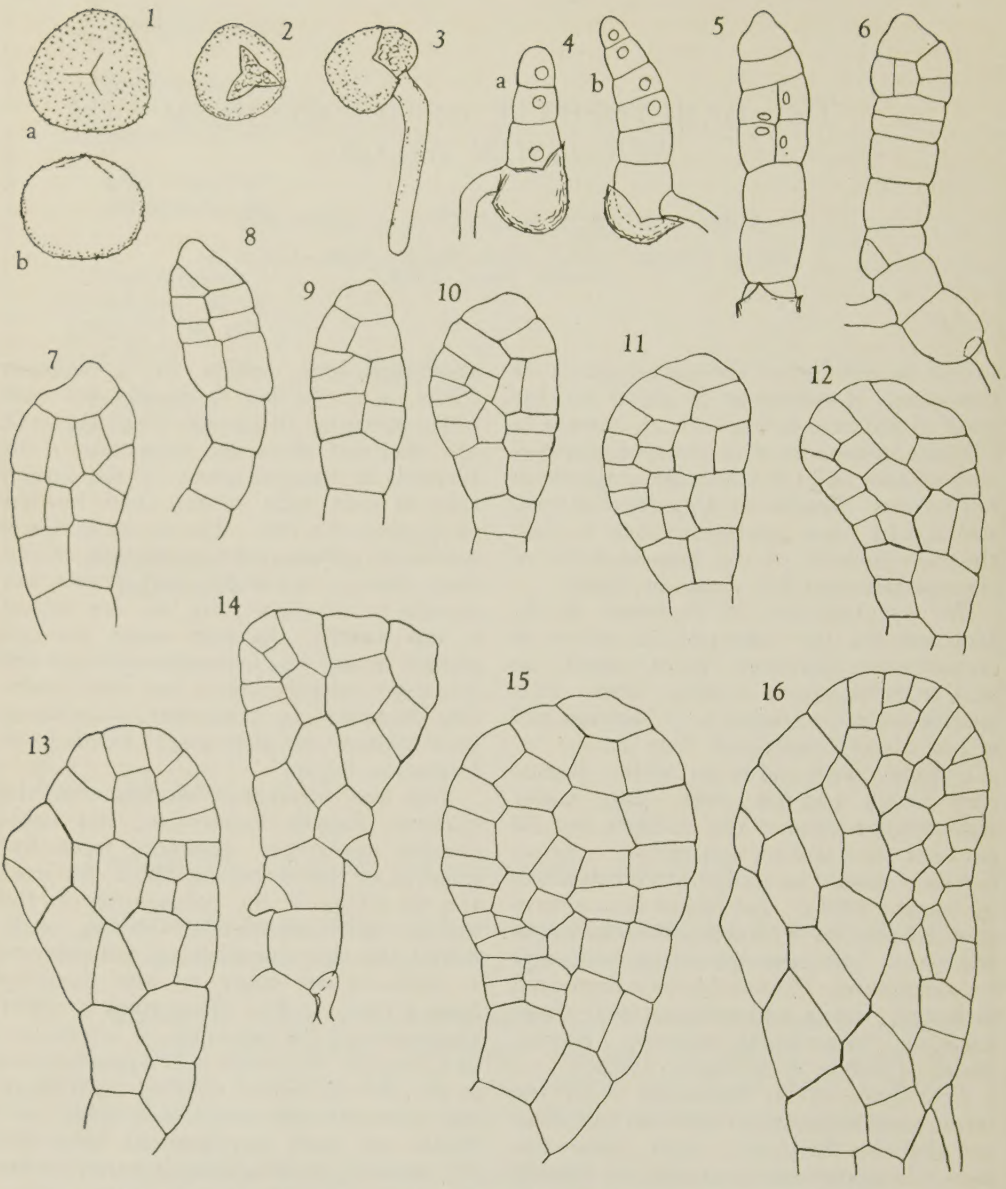
Our knowledge of the gametophyte of the genus *Acrostichum* is based on the work of Schumann (1915) on *A. aureum* L. This deals primarily with the sporophyte of *Acrostichum* and the acrostichoid species of *Leptochilus*, *Stenosemia* and *Stenochlaena*, which had been associated with it, and the development of the gametophyte of *Acrostichum* was not given in detail.

We are indebted to Professor R. E. Holttum for the collection of spores of *Acrostichum speciosum* Willd. which he sent from Singapore in May, 1950. This species is closely related to *A. aureum* and is not always separated from it.

Cultures were made on water, porous clay crock and on peat. Tap water was used for some of the cultures, but 50 per cent sea water for another set. *Acrostichum* is classed as a facultative halophyte by Gams (1938). Several of the cultures were watered for several months with dilute sea water, but later tap water was used for all cultures. The techniques employed in killing, fixing and staining were those used for *Stenochlaena palustris* (Burm.) Bedd. (Stokey & Atkinson, 1952a).

The spore of *A. speciosum* is of the tetrahedral type, approximately spherical or slightly flattened, light yellowish-brown in colour, with a spore coat slightly roughened by minute tubercles, and with an average diameter of 53 μ (Fig. 1*a*, *b*). The tripartite ridge is inconspicuous until germination. This occurs in 6-7 days with a splitting at the ridge; at this time granules are visible but not chloroplasts (Fig. 2). The first prothallial cell, which is green as it emerges from the spore coat, is then separated by a wall from the colourless rhizoid (Fig. 3). A series of cross-walls in the prothallial cell results in a filament (Figs. 4, 5) which is usually 6-8 cells but sometimes 10-12 cells long; the cells are relatively short and elongation of the filament is brought about by the formation of new cells rather than by the elongation of a few. The spores in dilute sea water germinated a little more slowly than those in tap water, and showed less growth in 12 days (Fig. 4*a*, sea water; *b*, tap water). In four weeks the difference in size was less noticeable but the sea water cultures were a less vivid green. The filaments in both sets of cultures grew to about the same length before plate formation began.

The first intercalary divisions in the filament, usually longitudinal but occasionally transverse, appeared most frequently in the second or third cell from the tip (Figs. 5, 6), occasionally in the fourth, and infrequently farther back. About this time the terminal cell assumes a characteristic more or less papillate form (Figs. 5, 6). This gives a slight suggestion of the beginning of a papillate hair, but no cross-wall ever appeared and in no case did a hair develop. Although the terminal cell becomes broader and flatter as plate development proceeds, its peculiar form makes it recognizable for a considerable period (Figs. 5-16). In some gametophytes a more or less oblique wall was formed in the terminal cell (Figs. 8, 10, 13), but no case was found in which any further divisions occurred with certainty. This occasional oblique division may have led Schumann, who gives only a few early stages, to describe the tip cell of the filament as an apical cell cutting off segments alternately right and left.



FIGS. 1-16 — Fig. 1*a*, *b*, spore. × 350. Fig. 2, germination. Fig. 3, first prothallial cell and rhizoid. Fig. 4, filaments 12 days old; *a*, 50 per cent sea water; *b*, tap water. Figs. 5-16, stages in development of plate and lateral meristem.

In the formation of the plate, the products of the third cell from the tip usually take the most active part (Figs. 7, 9, 12), but an important part may also be taken by the second cell, as indicated by the sequence of divisions in Figs. 10, 13 and 16; or the products of the second cell may take only a minor part (Fig. 14). The fourth cell from the tip usually contributes to the plate and even those farther back may do so, with the result that in the mature thallus there may remain only two or three undivided cells at the base. Whatever the variations in these

early stages the meristem region is developed as a truly lateral meristem. There was not found at any time a wedge-shaped apical cell which cuts off segments alternately right and left. The region which may become the marginal meristem is often indicated by the appearance of an oblique wall in one of the marginal cells (Figs. 7, 9, 10). The wedge-shaped cell thus formed elongates, and successive anticlinal walls give rise to a band of meristematic cells (Figs. 12, 13). The marginal meristem does not always arise in this way, but may be formed by other sequences of division (Figs. 11, 15). The marginal meristem which is lateral in origin may remain so for a varying period and the terminal cell will remain at the tip of the longitudinal axis, but the activity of the cells on the distal side of the meristem is so much greater than that of the proximal side that sooner or later the terminal cell is pushed into a lateral position (Figs. 13, 14). However, if the cells on the opposite side of the thallus, although undergoing fewer divisions, enlarge sufficiently, the terminal cell shows little or no shift in position at the early spatulate stage of the thallus (Figs. 11, 12, 15). With increasing growth of the gametophyte the difference between the proximal and distal sides becomes pronounced, and the gametophyte attains such an asymmetrical form as that of the 8-week old thallus in Fig. 17.

As development continues, a cushion forms behind the meristematic region; the section formed by the distal portion develops a large extended wing, B, which is in strong contrast to the small wing, A, formed by the proximal portion (Fig. 18). At this stage, which may be attained in 9-10 weeks, archegonia begin to appear; in this gametophyte there were spermatozoids in the neck of one archegonium. The thickening of the cushion may cause the wings to bend backwards in hinge-like fashion. If fertilization does not occur, the growth of the midrib and a certain amount of wing tissue continues indefinitely. The continued growth does not destroy the asymmetry (Fig. 19), but the formation of wings — at first unequal, later equal — on both sides of the cushion tends to make it less pronounced (Fig. 20). The original proximal wing of the thallus, A, always small at the base, may remain visible but inconspicuous throughout the life of the gametophyte; but the distal wing, B, remains conspicuous as a rounded " lobe " below the basal filament, *f*, which is perpendicular to the direction of growth of the thallus, and hence appears to be lateral (Figs. 19-21, 23).

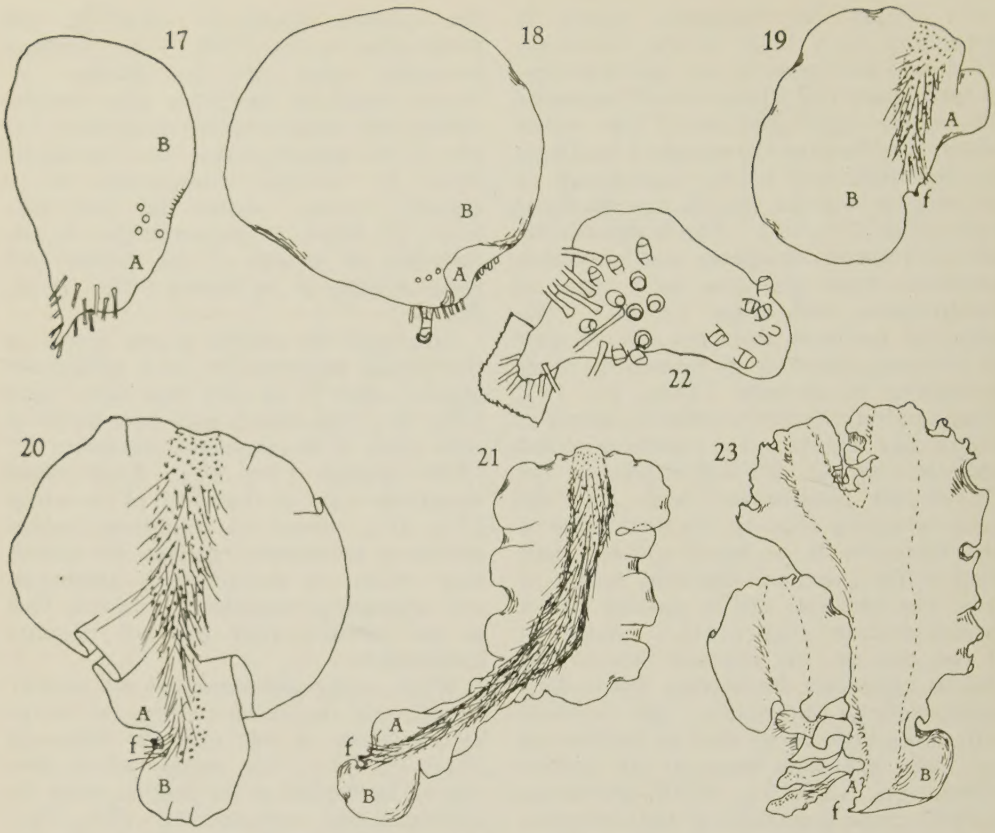
Although the midrib is not heavy in the young gametophyte and archegonia appear when it is only two cells thick (Fig. 35), the midrib may become 10-12 cells thick if development continues for 12-18 months (Fig. 46). Even when variations occur in the width of the wings (Fig. 21), related to conditions in the culture or to seasonal changes, the midrib may retain its characteristic thickness, and archegonia continue to develop but in our cultures they did not undergo fertilization.

While young gametophytes are usually smooth and regular in outline, the wings become more or less irregular with age (Figs. 21, 23). The wings, which develop on both sides of the midrib, may be approximately symmetrical (Fig. 20); in our material they never projected much, if at all, beyond the midrib, and during the winter the midrib usually projected beyond the wings (Fig. 21).

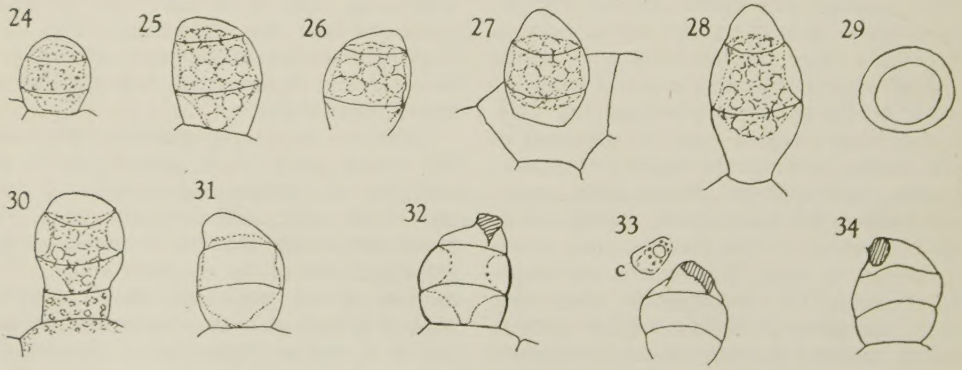
Old gametophytes may give rise to regenerated branches, especially near the base (Fig. 23); these may be of irregular form and bear only antheridia (Fig. 22), or grow more extensively and develop as a more or less symmetrical branch with an archegonial cushion.

Rhizoids on young gametophytes and the young parts of old gametophytes are pale tan in colour, but darken to deep tan with age. Chloroplasts were not found in young rhizoids even on young gametophytes of the filament stage. The midrib of old gametophytes is covered with a heavy growth of tangled rhizoids but it is not so dense as to conceal the archegonia.

Hairs were not found on the gametophyte of *A. speciosum* at any stage of its development.



FIGS. 17-23 — Fig. 17, thallus with antheridia, 8 weeks old. Fig. 18, thallus, 10 weeks old; A, proximal region; B, distal region. × 13. Fig. 19, thallus, 4 months old; *f*, basal filament. × 6. Fig. 20, thallus, 13 months old. × 6. Fig. 21, thallus, 20 months old, × 3. Fig. 22, regenerated branch from base of thallus, 15 months old. Fig. 23, branched thallus, 15 months old.



FIGS. 24-34 — Antheridium. Fig. 24, young antheridium. Figs. 25-27, antheridia almost mature. Figs. 28, 30, old antheridia which have failed to open. Fig. 29, cap and ring cells. Fig. 31, antheridium shortly before opening. Figs. 32-34, antheridia which have discharged their contents; *c*, cap cell. × 225.

Antheridium

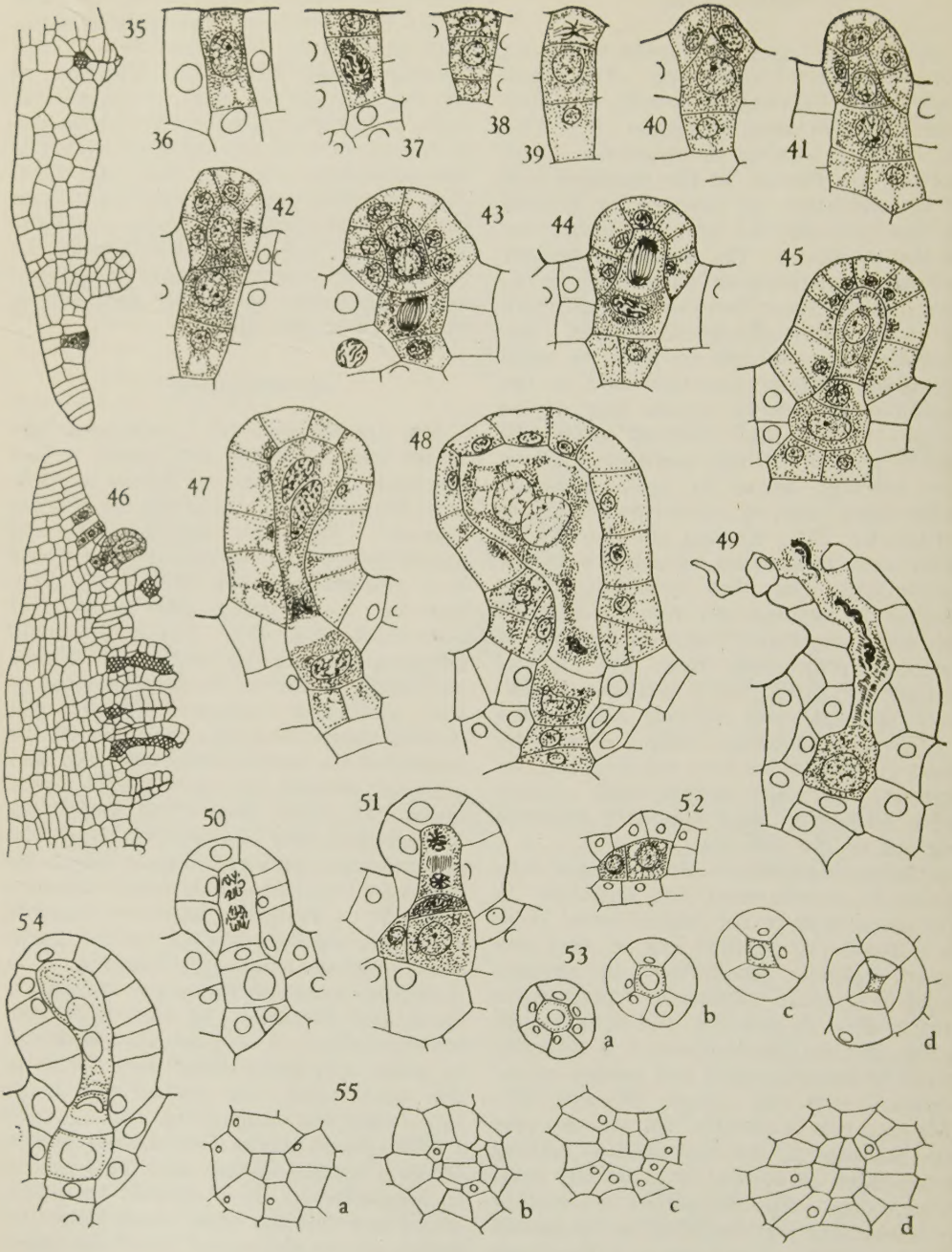
Antheridia began to appear when our cultures were 6-7 weeks old. The gametophyte at this stage is broadly spatulate with an active lateral meristem (Fig. 17). In such a thallus a relatively small portion has formed on the proximal side of the meristem, A; most of the thallus, B, has been derived from the distal side of the meristem. The antheridia appear behind the meristem or between the meristem and the base; there may be as many as 15-20 before archegonia appear. Antheridia may continue to form for some time, but usually sparingly and in the region which belongs to the base of the larger wing — that derived from the distal portion of the meristem. When our cultures began to age, antheridia were found only on regenerated branches (Figs. 22, 23). During the summer of 1951 such antheridial branches were not uncommon, but they ceased to form during the autumn and winter. Antheridia were sometimes found on disc-like or bulbous projections from the ventral surface (Fig. 30), as in *Blechnum buchtienii* Rosenst. and various other ferns (Stokey & Atkinson, 1952b). Ameristic male gametophytes were not found in our cultures, but thin slender thalli usually with antheridia were found in crowded regions of the cultures.

The antheridium in *A. speciosum* conforms in development and structure to the usual type in the higher ferns; there is a basal (or funnel) cell, a ring cell and a cap cell. The form of the antheridium is unusual. Before it is mature the antheridium is globular and symmetrical (Fig. 24), but at maturity it is typically more or less elongated and has an asymmetrical cap cell (Figs. 25, 26, 31). The cap cell is usually high on one side and flattened on the opposite side making a lop-sided structure; it is usually relatively large (Fig. 29). The asymmetry of the cap cell was described by Schumann for *A. aureum*. There was no antheridium seen in which the cap cell was divided. A heavy layer of cutin is present on the antheridium wall, and that on the cap cell persists as a ragged structure after dehiscence (Figs. 32-34). At dehiscence there is a break in the cutin on the high side of the cap cell, and the spermatocytes may be seen to pour out through the opening in the cutin. The discharge of the cap cell was not seen, but in several cases a delicate evanescent cell was seen in the vicinity of the opening and this was presumably the cap cell (Fig. 33c). The fact that few cap cells were seen suggests that perhaps in many cases the delicate cap cell is ruptured during the more or less violent process of dehiscence, as in *Blechnum buchtienii*, and is not thrown off as one piece.

Archegonium

The archegonium of *A. speciosum* develops from an initial cell found, in our material, in the fifth to eighth segment from the meristem, usually in the seventh segment (Fig. 46). On 4-month old gametophytes the initials may be found in a cushion two cells thick (Fig. 35), but on a 14-month old it is four cells thick (Fig. 46). The archegonium develops in the usual way (Figs. 36-45) with some variations in the behaviour of the neck-canal nucleus. Usually this divides before the central cell cuts off the nucleus of the ventral canal cell (Fig. 43) although division may start in each cell at about the same time (Fig. 44). One archegonium was observed in which the ventral canal cell was complete before the neck-canal nuclei had completely reformed (Fig. 51). Frequent cases were found of a second nuclear division in the neck-canal nucleus (Fig. 50) resulting in a 4-nucleate canal, as may occur in *Stenochlaena* and *Blechnum*, as well as in the lower families. Two cases were observed in which only three nuclei were visible in the neck canal, the central one being larger than the others (Fig. 54). Conard (1908) found this in *Dennstaedtia punctilobula* (Michx.) Moore and we found it in *Stenochlaena*. It is difficult to understand how this has come about unless by fusion of two of the four nuclei described above.

The mature archegonia exhibit considerable difference in size (Figs. 47, 48). They are inclined slightly toward the posterior end of the thallus (Figs. 35, 46)



FIGS. 35-55 — Archegonium. Fig. 35, l.s. gametophyte, 4 months old. Figs. 36-45, development of archegonium. Fig. 46, l.s. gametophyte, 14 months old. Figs. 47, 48, mature archegonia. Fig. 49, open archegonium, spermatozoids in neck. Figs. 50-52, 54, anomalies. Fig. 53, c.s. neck; *a*, *b*, *c*, serial sections through neck-canal nuclei; *d*, through base of neck. Fig. 55, c.s. mature archegonia at level of basal cells.

and show a varying number of cells in the neck tiers, the most common being five and six (Fig. 47). As in other higher ferns, the end of the neck becomes bulbous (Figs. 35, 48), the cells at the tip being thinner than those near the venter (Figs. 47, 48, 54). The four tiers of neck cells divide periclinally at the base of the neck (Figs. 48, 53*d*). Cross-sections in the region of the neck-canal nuclei where anticlinal divisions occur show 4-6 cells (Fig. 53, *a-c*). The basal cell divides during the development of the archegonium so that the mature egg rests directly on two, three or four cells as is shown by cross-sections through that region (Fig. 55, *a-d*). In longitudinal sections only one or two basal cells are seen, depending on the direction of the cut (Figs. 43, 45). The prothallial cells adjacent to the egg also divide, and with the basal cells they provide a two-layered ventral jacket (Fig. 48). The neck-canal nuclei increase greatly in size (Figs. 45, 47, 48), and then, as is usual, disintegrate along with the ventral canal cell.

Discussion

The genus *Acrostichum* is interesting from several points of view: its widespread distribution in the coastal regions of tropics and sub-tropics; its adaptation to brackish water, the only fern characteristic of brackish swamps; the vicissitudes of its classification during which it has shrunk from a genus of over a hundred species (Hooker & Baker, 1868) to the present residue of 1-4; and the question of its origin and relationship. It shows no close affinity to any other group. Christensen (1938) grouped it with *Neurocallis* and *Stenochlaena* under " Acrostichoid genera probably derived from the Pteridoideae". Holttum (1949) treated it as a member of the Pteridoideae in his Dennstaedtiaceae. Copeland (1947) placed it in his Pteridaceae and considers its affinity to *Pteris* as the most probable. Ching (1940) related it to Aspidioid ferns and placed it in a separate family, the Acrostichaceae, with *Neurocallis*. Dickason (1946) also recognized the Acrostichaceae but he allied the family with the Gymnogrammaceae.

It may be assumed that no fern would attain world-wide distribution if it did not have spores which germinate readily under a wide range of conditions into gametophytes of vigour and adaptability. Schumann (1915) made some tests with solutions and found that spores did not germinate on a solution of NaCl alone, but did germinate on a solution of NaCl and KCl although growth soon ceased; they germinated on Knop's solution with NaCl and developed normally but were paler in colour than on other media. This is similar to the results which we obtained with peat and dilute sea water. The gametophyte, like the sporophyte, appears to be a facultative halophyte, and while it may complete its life cycle as a halophyte, growth is better on the usual substrata for ferns. It attained maturity in 9-10 weeks in this latitude but in the higher temperatures of the tropics the gametophyte probably arrives at maturity more quickly. The gametophyte of *Acrostichum* is a vigorous one and may become notably large; and even if the old gametophytes do not always bear functional antheridia and archegonia, they bear regenerated branches which may do so.

The morphological characters of the gametophyte which are of special interest are: (a) lack of hairs; (b) the development of a lateral meristem region — not a wedge-shaped apical cell—and a permanent asymmetrical form; (c) the asymmetrical antheridium. The lack of hairs seems to be a characteristic of the Pteroid group: Lagerberg (1906) did not give them for *Pteridium aquilinum* (L.) Kuhn; they are not described for *Pteris* in the various incomplete accounts of a considerable number of species; they are lacking, in general, in the Cheilanthoid (Gymnogrammoid) ferns (Stokey, 1951). This is not a character of great weight unless there is constancy in the group, and we do not know the gametophytes of enough Pteroids to know how constant it is in that group. The asymmetrical gametophyte has been found in several genera of higher ferns, most of them Cheilanthoid (Stokey, 1951). Goebel (1930) reported it in *Pteris longifolia* and gave it as his opinion that it is without genetical significance, since both a lateral and a terminal

meristem may be found in the same species. (He refers to Klebs who said that under certain conditions an apical meristem may appear in *P. longifolia.*) It is necessary to distinguish between the permanent asymmetry of *Acrostichum* which is apparently like that of *P. longifolia,* and the temporary asymmetry found in certain species. In the latter the prothallial filament may develop a papillate hair on the terminal cell and the wedge-shaped apical cell will develop laterally making the gametophyte asymmetrical for a short period, but eventually it becomes symmetrical (Döpp, 1927; Stokey & Atkinson, 1952, a & b). It is possible that both temporary and permanent asymmetry may be of genetical significance in some cases, but it is essential to distinguish between the two types. Permanent asymmetry has not been reported for any of the Aspidioid ferns.

The asymmetrical antheridium of the *Acrostichum* type has not been reported for any other fern, and so far as we know at present, it is a peculiarity of *Acrostichum.*

In the germination stage it is of interest that the elongation of the filament is brought about by the formation of many cells and not the elongation of a few. The latter is usually associated with advanced ferns — it is a quicker and more economical method — but there may be no significance in the series of short conspicuously green cells in *Acrostichum.* The development of the papillate cell on the tip of the prothallial filament, which was a constant character in our material, was not mentioned by Schumann but is suggested by her drawing 3B. It may possibly indicate an ancestry with hairs on the gametophyte, or, like the cap cell of the antheridium, may be a specific or generic character.

There is, therefore, nothing in the gametophyte structure or development which would indicate a close affinity with the Aspidioid ferns, but there are several characters which would ally it with the Pteroid ferns, and, more particularly with the Cheilanthoid group.

Summary

Germination of the spore of *Acrostichum speciosum* occurred in 6-7 days on tap water and a little later on 50 per cent sea water; a filament was formed, usually of 6-8 cells; the terminal cell has a slight but characteristic papilla, although no hairs are borne on the thallus at any stage. The meristem is formed laterally by a group of initials. The development of the plate is asymmetrical with a large and a small wing; in 12-20 months the thallus became symmetrical except for the base. Antheridia are somewhat elongated with an asymmetrical cap. The archegonium develops in the usual manner but with some variation in the time of division of the neck-canal nuclei; cases of 4 neck-canal nuclei were not unusual, and 3 were also found.

Part of this investigation was carried out by the senior author at the Marine Biological Laboratory, Woods Hole, Mass.

The junior author wishes to express her gratitude to the Biology Department, Amherst College, Amherst, Mass. for certain materials and use of apparatus.

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MORPHOLOGY OF THE SUBTERRANEAN ORGANS OF *ERYTHRONIUM JAPONICUM* AND ITS ALLIES[1]

YUDZURU OGURA

Botanical Institute, University of Tokyo, Japan

The genus *Erythronium* (Liliaceae) includes only a few species. The Japanese species, *E. japonicum* Decne., is very similar to the European, *E. dens-canis*, and it was once considered to be identical with the latter or given a varietal rank—*E. dens-canis* var. *japonicum* Bak. However, it is distinguished from the European species by having at the base of the subterranean organ a curious appendage, which is absent in the latter.

The subterranean organ of *Erythronium* is either spherical as in *E. americanum*, or elongated as in *E. dens-canis*. In some species, such as *E. dens-canis*, *E. americanum*, *E. albidum*, *E. grandiflorum*, *E. propullans*, it gives out a long runner which produces a new individual at its tip, as reported by Irmisch (1863), Gray (1871), Blodgett (1894-95, 1900), Robertson (1906), etc. Such a runner has also been denoted as stolon, dropper, or sinker, but it has never been observed in *E. japonicum*, in which its place is taken by the curious appendage mentioned above.

During 1949-51 the writer studied the morphological characters of the subterranean organ and the mode of its growth in the Japanese species, as these characters have not yet been investigated. He also studied, for comparison, the morphological characters of the subterranean organs of certain allied species, especially *Tulipa edulis*, *T. latifolia*, *Gagea japonica* and *Lloydia triflora*. Materials for the investigation were collected in the suburbs of Tokyo, and some plants were kept in cultivation for closer observation.

External Characters

The subterranean organ is long and club-shaped and whitish in colour. It is 50-70 mm. in length and 5-10 mm. in breadth. The lower portion is globular or somewhat pointed, and bears some thin roots. The upper portion becomes thin and passes into the petiole in the non-flowering plant (Fig. 1*B*), and into the floral stalk in the flowering plant (Fig. 1*A*). The appendage consists of a few segments resulting from the accumulated remains of the annually formed basal parts of successive years, some of the segments becoming connected to form an irregular chain (Fig. 1*D-G*). The form of a segment

1. Contribution (N.S. No. 58) from the Division of Plant Morphology, Botanical Institute, Faculty of Science, University of Tokyo.

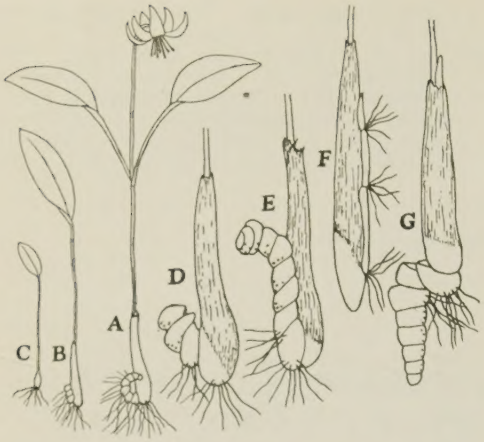

FIG. 1 — *Erythronium japonicum* (in April at Tokyo). *A*, flowering specimen; *B*, non-flowering specimen; *C*, young plant; *D-G*, various forms of bulbs with appendages and roots. *A-C* × ca. $\frac{1}{4}$; *D-G* × ca. $\frac{2}{3}$.

and the mode of its connection with its neighbour are very variable. As a rule each segment is more or less hemispherical. The youngest is attached to the mother axis with its broader face. The second segment is attached to this in the same manner, and so on. If the segments were similar, the appendage would have a regular form, but as they are not always similar in shape or size, the appendage becomes curved and twisted. Although the number of segments is not constant, it is usually below ten. Sometimes the segments are very slender, and are then in contact with the lateral surface of the mother axis (Fig. 1*F*). Roots come out close to the lower side of the segments.

The young plant is vegetative and has a foliage leaf, whose long petiole continues to the upper part of the subterranean organ (Fig. 1*C*). Larger plants may be in the non-flowering (Fig. 1*B*) or flowering condition (Fig. 1*A*). In the latter case a long floral stalk, with a large flower at its top and two foliage leaves in its middle region, continues to the upper part of the subterranean organ. Near Tokyo, the leaves or floral stalks begin to appear above the ground at the end of February or the beginning of March, and wither completely in May. The subterranean organ is clothed with a pale brown skin, which decays and disappears at a later stage.

Internal Structure

Although the internal structure of the subterranean organ does not differ essentially in the non-flowering and flowering individuals, they are separately described for convenience.

Taking the non-flowering individuals first (Fig. 2*A*), a cross-section of the subterranean organ shows a circular outline with an arc-shaped slit in its centre. This slit is originally a cavity, but later becomes pressed into such a shape. In the lower portion is a small process, situated at the bottom of the cavity, which forms the bud for the next year (Fig. 2*A*, *b*). In the upper part also, which is enclosed within the petiolar base, there is a small process whose structure shows it to be an unfolded lamina (Fig. 2*A*, *f*), and the above-mentioned slit terminates in this process. From a comparison of the cross and longitudinal sections, we may conclude that a subterranean organ consists of two layers of leaf sheaths, an outer thin and an inner thick layer, which are, however, fused to form a common structure for the most part (Fig. 2*A*, *t*). The inner sheath is penetrated by a slit-like cavity including a basal bud, and its upper part becomes transformed into an unfolded lamina. The outer sheath covers this and its upper part elongates into a petiole, while the main part fuses completely with the inner sheath. The cavity of the outer sheath, which is seen only at the upper end, continues to the adaxial surface of the petiole. A pale brown layer, which envelops the outer part in the early stage, forms the remains of the common sheath of the former year, and consists of disorganized cells without any starch grains (Fig. 2*A*, *c*).

Thus, the subterranean organ may be considered as a kind of the tunicate bulb, consisting of two fused foliar sheaths. In flowering individuals the bulbs may consist of three sheaths, as will be described below.

The whole tissue consists of starch-filled parenchyma and is traversed by

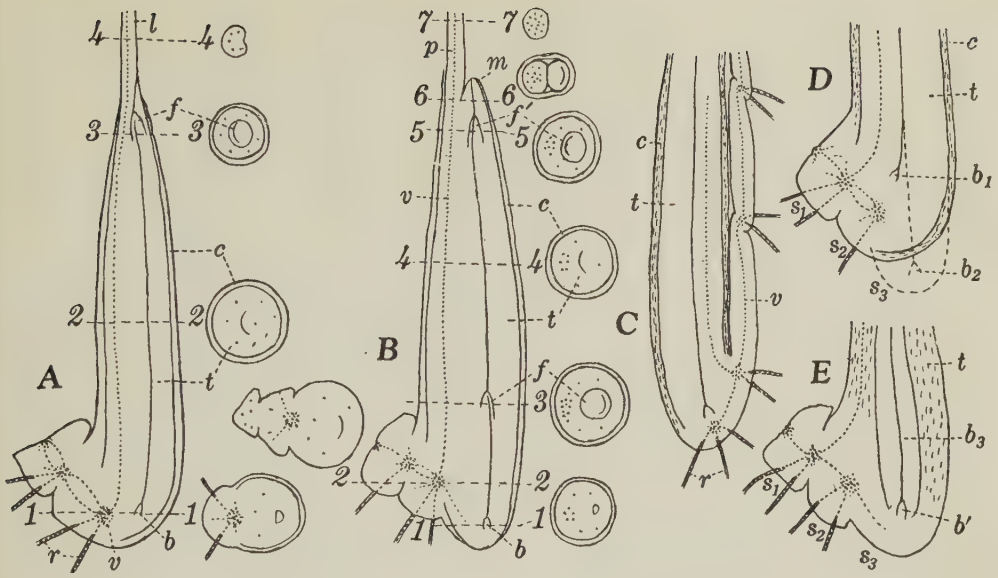

FIG. 2 — *Erythronium japonicum*, longitudinal and transverse sections of bulbs showing their construction and mode of growth. *A*, non-flowering specimen. *B*, flowering specimen; 1, 2-7 indicate cross-sections at the levels 1, 2-7; *C*, non-flowering plant of the type shown in Fig. 1, *F*; *D-E*, diagrammatic figures showing the mode of growth of the bulb; *D*, showing the condition at the beginning of April (in full line) and at the end of April (in broken line); the bud b_1 changing its position to b_2; *E*, showing condition in February of following year; bud b_2 has grown into b_3 and b′ is a new bud; (*b*, b_1, b_2, b_3 = bud; *c* = cover sheath; *f*, *f′* = unfolded lamina; *l* = foliage leaf; *m* = process of sheath; *p* = floral stalk; *r* = root; s_1, s_2, s_3 = segments or remains of basal parts of sheaths in successive years; *t* = sheath; *v* = vascular bundle).

longitudinally running vascular bundles, some of which enter the petiole. In the lower part the vascular bundles aggregate into a mass. This part is the real base of the whole organ, though it is not situated in the lowest region, and the internal bud is not always situated near this. The root traces go out from this vascular mass in various directions (Fig. 2*A*, *r*).

Each segment of the appendage corresponds in structure to the basal part of the sheath, being filled with starch grains and penetrated by vascular bundles and root traces.

Turning to the flowering individual (Fig. 2*B*), here also a cross-section of the subterranean organ shows a circular outline and an arc-shaped slit, but we see three processes within the organ: the first in the lowest part (Fig. 2*B*, *b*), the second somewhat above (Fig. 2*B*, *f*), and the third in the uppermost part (Fig. 2*B*, *f′*). The first is the bud for the following year, while the second and the third are unfolded laminas. The whole structure consists, therefore, of three layers of sheaths, a small inner, a thick middle, and a thin outer sheath, but they fuse together in their main part into a common sheath (Fig. 2*B*, *t*). Another characteristic of the flowering individual is that the upper part of the bulb shows two parts. One of these elongates into the floral stalk (Fig. 2*B*, *p*), while the other remains as a small process (Fig. 1*A*, *E*, *G*; Fig. 2*B*, *m*). Camparing this with an allied species, *Gagea japonica*, in which this part elongates into a foliage leaf (cf. Fig. 5*A*), we may conclude that this process really represents the apex of the outermost sheath, which does not develop into a leaf. The whole organ is covered in early stages with a pale brown membrane (Fig. 2*B*, *c*), which later decays and disappears.

The common sheath is rich in starch and is traversed by longitudinally running vascular bundles. The bundles in the floral stalk, ten or more in number, are roughly arranged in two concentric circles, which run down into the outer sheath of bulb, so that at each level of the bulb a group of bundles is to be seen (Fig. 2*B*). This feature enables one to distinguish quite easily a cross-section of the bulb of a flowering individual from that of a non-flowering one even when the leaves or flowers have shed.

Growth of the Subterranean Organ of Erythronium japonicum

In Tokyo, the leaves of the plant begin to appear above the ground at the end of February or the beginning of March, and the flowers from the end of March to the middle of April. After the flowering season, the leaves and flowers wither completely leaving only the fruiting stalks in which the seeds ripen in June.

The characteristics of the bulb described above are seen in the flowering season. Early in this season, on the pale brown cover of the previous year, an obliquely oriented border may be recognized on its basal part (Fig. 1*D, F*). The upper part becomes somewhat transparent, soft and wrinkled, and gradually decays away, but the lower remains unaltered. Meanwhile, the basal part of the bulb elongates laterally and projects through the cover (Fig. 2*D*, s_3, broken line). That is why the new segment is situated laterally to the elongating tip. Usually such basal elongation is slight, but in extreme cases it is very prominent and the lower part elongates in the form of a horn (Fig. 2*C*). In the latter case the form of the remaining segment becomes very irregular.

After the leaves and flowers wither away the form of the bulb remains unchanged until next spring. In the spring, the development of the bud within the bulb begins as early as January or February. As it elongates, it passes through the central slit of the bulb. Towards the end of February it penetrates the upper part of the bulb, and in the beginning of March it appears above the ground. At this stage, the elongating bud is thin, but is full of starch, while the sheath of the bulb gradually loses its starch and tends to become soft and transparent (Fig. 2*E*). Soon after, the upper part of the bud elongates further and expands into a foliage leaf or a floral stalk. At the same time the foliage leaf or the floral stalk thickens, while the older sheath becomes thinner and pale brown.

From the observation on the growth of the bulb, in flowering as well as non-flowering individuals, it is clear that the downward growth of the bulb becomes arrested by the fusion of the leaf sheaths, and this results in the abnormal growth. It proved very difficult, however, to understand the mode of this abnormal growth until the writer was able to compare it with the formation of the runners in two species of *Tulipa*, whose morphological characters may be described below.

External and Internal Morphology of the Subterranean Organs of Tulipa

Two species of *Tulipa*, *T. edulis* Bak. and *T. latifolia* Makino, are found near Tokyo. Both flower at about the same time as *Erythronium japonicum*. The writer was able to study the external and internal structure of the subterranean organs as well as the process of formation of the runners, whose presence has been observed by many authors, such as Irmisch (1850, 1863), Masters (1869), Gray (1871), Loret (1875), Blodgett (1894-95, 1900), Robertson (1906), Arber (1925), Goebel (1928), Troll (1937), Raunkier (1937), etc., in *T. silvestris*, *T. saxatilis*, *T. praecox*, *T. biflora*, etc., and species of *Erythronium*. The mode of formation of this organ has been investigated by Loret, Blodgett, Robertson and others, and it was sometimes designated as a dropper or sinker. Since my observations agree with those of the above authors, they may be described briefly.

The external and internal structure of the subterranean organs of the two species is essentially similar (Figs. 3, 4). The subterranean organ is nearly spherical, and has a thin membranous cover. This cover, which forms the remains of the sheaths of the previous year, becomes

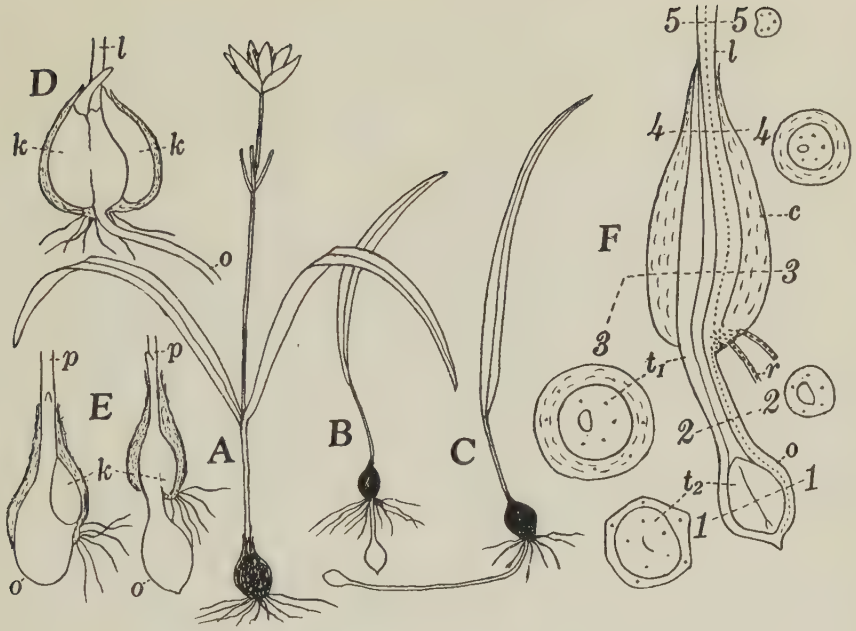

FIG. 3 — *Tulipa edulis* and *T. latifolia* (in April at Tokyo) *A*, flowering specimen of *T. latifolia; B*, non-flowering specimen of *T. latifolia* with a runner; *C*, same of *T. edulis; D*, bulb of *T. edulis* with outer cover removed, showing main bulb, runner and two bulblets; *E*, bulbs of *T. latifolia* with outer cover removed, showing early stage in formation of a runner; each bulb has a bulblet; *F*, longitudinal and transverse sections of bulb of non-flowering *Tulipa*, showing construction of runner (cf. Fig. 4*A*); 1, 2-5 are cross-sections at levels 1, 2-5; (*c* = cover sheath; *k* = bulblet; *l* = foliage leaf; *o* = runner; *p* = floral stalk; *r* = root; t_1, t_2 = sheath; *v* = vascular bundle.) *A-C* × ca. $\frac{1}{4}$.

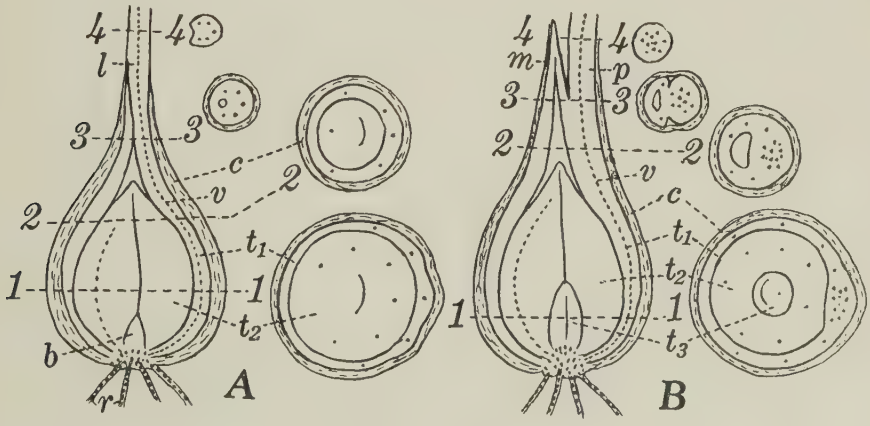

FIG. 4 — *Tulipa edulis* and *T. latifolia*; longitudinal and transverse sections of bulbs.; *A*, non-flowering specimen of *T. latifolia*; *B*, flowering specimen of *T. edulis*; 1, 2-4 represent cross sections at level 1, 2-4; (*b* = bud; *c* = cover sheath; *l* = foliage leaf; *m* = process of sheath; *p* = floral stalk; *r* = root; t_1, t_2, t_3 = sheath; *v* = vascular bundle).

separated irregularly into a few layers, of which the outermost is black. The upper part tapers gradually and continues in the non-flowering plant into a foliage leaf (Fig. 3*B*, *C*). In the flowering individual it elongates into a floral stalk bearing two foliage leaves (Fig. 3*A*). At the base of the floral stalk is a small process, which is longer in *T. edulis* than in *T. latifolia* (Fig. 3*E*). The roots emerge from the bottom of the subterranean organ which is of nearly the same size in both species, being 10-12 mm. in diameter. The size of the foliage leaf is also the same, being 6-9 mm. in breadth and 15-25 cm. in length.

A study of the transverse and longitudinal sections of the subterranean organ clearly shows that it is a bulb consisting of two or three layers of thick sheaths (Fig. 4*A*, *B*). In a non-flowering specimen, it consists of an outer thin (Fig. 4*A*, t_1) and an inner thick sheath (Fig. 4*A*, t_2). The latter includes in its centre a small bud, while the upper part of the former transforms into a petiole. In a flowering specimen, it consists of an outer thin (Fig. 4*B*, t_1), a middle thick (Fig. 4*B*, t_2) and an inner small sheath (Fig. 4*B*, t_3), and the latter includes a bud in its centre. In the upper region, the outer sheath is divided in two parts, one elongating into the floral stalk (Fig. 4*B*, *p*) and the other forming a hollow process (Fig. 4*B*, *m*). In either case a cross-section shows an arc-shaped slit in the centre, and each sheath, which is full of starch grains, is traversed longitudinally by vascular bundles. In the flowering specimen the floral stalk includes a number of vascular bundles, which pass down to the outer sheath. Each sheath is thus completely separate and the typical bulb-like construction is very clear. The number of sheaths agrees with that in *Erythronium japonicum*, and this is the reason for considering that the subterranean organ of the latter is derived by a coalescence of sheaths of the *Tulipa* type. The previous year's covering membrane consists of disorganized tissues which are devoid of starch grains. On the inner side of the sheath there are long unicellular hairs.

In both species large or small knots are found round the bulb. Each knot is attached by a narrow base to the surface of the sheath or the surface of the cover. The size, form and number of knots is variable. When small, a knot is not noticeable under the cover, but when it is large, it breaks out of the cover and becomes as large as the main bulb (Fig. 3*D*, *E*). It is connected with the sheath but not with the stem base. Between the place of attachment and the stem base there is a small ridge on the sheath. This suggests that the basal part of the small knot is fused with the surface of the sheath. Each knot resembles a bulb in its construction, and may be denoted as a bulblet.

In the flowering season, i.e. from the end of March to the beginning of April in Tokyo, we see a white runner, 2-3 mm. in diameter, emerging from the bottom of the bulb (Fig. 3*B*, *C*). It continues to elongate day by day, and its tip thickens gradually, until at the end of April it becomes an ovoid body. In *T. latifolia* the runner is only about 2-3 cm. in length, and runs downward (Fig. 3*B*), but it is much longer in *T. edulis*, about 10-15 cm., and runs horizontally (Fig. 3*C*). In the latter species the longest runner was found to measure 21 cm.

The runner is a slender, hollow tube, including a long cavity, which is circular or semicircular in cross-section (Fig. 3*F*, 2). The tip is massive and shows the characters of a small bulb, consisting of a thin outer sheath and a thick inner one, including a small bud within it (Fig. 3*F*, 1). The outer sheath is the continuation of the runner, while the inner corresponds in its construction with that of the mother bulb. At the bottom of the latter there is a hard tissue consisting of a mass of vascular bundles, from which the roots go out. This represents the stem base, and it is from its lateral part that the runner takes its origin (Fig. 3, *E*). In this case, the thick inner sheath with a bud protrudes outwards accompanying the outer sheath. Then, the latter elongates rapidly as a runner, including the inner sheath in its tip. Therefore, not only the runner, but also the mother bulb, is penetrated by a cavity which runs up to the petiolar base. Thus the bud of the mother bulb becomes included in the tip of the runner.

The writer's observations concerning this curious mode of formation of the runner agree with those of Blodgett (1900) and Robertson (1906). The development of the runner ceases at the end of April. It has no roots, and it is in the following spring that the tip develops into a new plant.

The formation of the runner is easily observed in non-flowering specimens (cf. Robertson, 1906), but in a few cases the writer also observed its formation in flowering specimens of *T. latifolia*. From the construction of the bulb it appears that the formation of the runner is possible in both individuals. Normally, one runner is produced from a bulb, but cases with two or more runners have also been recorded by Blodgett and Robertson in some species of *Erythronium* and *Tulipa*, although details have not been given. The writer observed a few cases with two runners. In one case, a single runner had bifurcated in its course; in another a second runner had come out of the bulblet beside the normal runner.

Functionally the runners of *Erythronium* and *Tulipa* are probably similar to other runners, but since their morphological nature is quite different, they might be designated as "foliar" runners.

In the construction of the bulb and the mode of attachment of the foliage leaf and floral stalk to the bulb, the two species of *Tulipa* are very similar to *Erythronium japonicum*. Though the abnormal growth of the bulb of the latter is very characteristic, the writer considers it to be comparable with the runner formation of *Tulipa*. In *Erythronium* the growth begins like that of a runner, but owing to the fusion of the outer and inner sheaths, runner formation cannot take place, so that the basal part enclosing the bud protrudes only slightly (Fig. 2*D*).

The garden tulip, *T. gesneriana*, which is cultivated abundantly in Japan, is essentially similar to the two species mentioned above, but differs in the following morphological features. Its bulb is much larger and consists of 4-5 thick sheaths. It is clothed with some brownish layers, and in the centre of the innermost sheath there is found an arc-shaped slit (Fig. 5*C*). In a non-flowering specimen the upper part of the outermost sheath elongates into a foliage leaf, while in a flowering one the outermost sheath is only a process (Fig. 5*C*, *m*), and a thick floral stalk proceeds directly out of the stem base, without any connection with the sheath as indicated in some text books (Fig. 5*C*, *p*). This is the second point in which the garden tulip differs from the two wild species, which are devoid of any independent floral stalk. A few small bulblets are produced from the stem base, and they become as large as the mother bulb, so that two or more large bulbs are enclosed within a common cover.

Blodgett (1900) and Robertson (1906) reported the presence of runners in the garden tulip, but the writer has never seen them.

It is not clear whether the floral stalk of other species of *Tulipa* or *Erythronium* arises independently from the stem as in the garden tulip, or it is fused with the sheath as in *Tulipa edulis*, *T. latifolia* and *Erythronium japonicum*. According to the figures given by some authors *T. praecox* shows a floral stalk of the type of the garden tulip.

Morphology of the Floral Stalk

As stated above, the subterranean organ of *Erythronium japonicum* is considered to be comparable with that of *Tulipa edulis* and *T. latifolia* and may be regarded as a modified bulb. It is also noticed that the bulb of these species is provided with a floral stalk which is closely connected with the leaf sheath. These characters have not been clearly described in *Erythronium* and *Tulipa* by previous investigators.

In most of the Liliaceae, provided with a bulb, the stem is short or massive. In non-flowering bulb, scaly or tunicate leaves are arranged on the stem in concentric circles, enclosing a bud in the centre, while in the flowering one, this bud elongates into a long stalk, on which foliage leaves and flowers are borne. The base of this stalk is thus attached directly to the stem. In this character, *Erythronium japonicum*, *Tulipa edulis* and *T.*

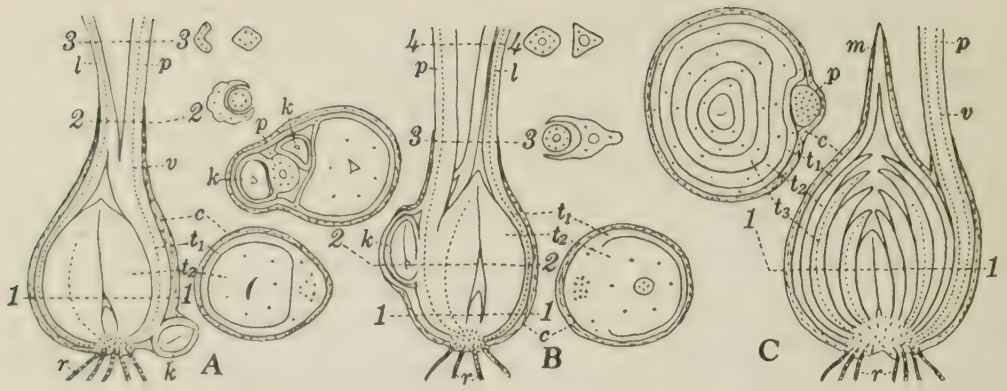

FIG. 5 — Longitudinal and transverse sections of bulbs of flowering specimens of *Gagea japonica* (*A*), *Lloydia triflora* (*B*) and *Tulipa gesneriana* (*C*); 1, 2, 3, 4 represent cross-section at levels 1, 2, 3, 4; (*c* = cover sheath; *k* = bulblet; *l* = foliage leaf; *m* = process of sheath; *p* = floral stalk; *r* = root; t_1, t_2 = sheath; *v* = vascular bundle).

latifolia are exceptional, as their floral stalk is a continuation of the upper portion of the leaf sheath. This sheath is the outermost layer of the bulb and corresponds to that provided by a foliage leaf in the non-flowering individual.

The floral stalk is generally cauline in nature, but in these species its basal part becomes transformed into a sheath of foliar nature. In this respect these species suggest some problems concerning the morphology of the floral stalk, which may be interpreted in two ways. According to one view, the floral stalk is a modified part of the sheath, while according to another, its lower part may be regarded as completely fused with the sheath. At first the writer favoured the first interpretation but since observing the transitional forms in the bulbs of allied species like *Gagea japonica* and *Lloydia triflora* he considers the second view to be more plausible.

Gagea japonica Pascher, from Karuizawa, which flowers in May, is a small herb possessing a small bulb clothed with a black cover. The structure of the bulb is quite like that of *Tulipa edulis* or *T. latifolia*, consisting of two or three layers of sheaths. In the non-flowering plant the outermost sheath elongates into a foliage leaf. In the flowering plant the same sheath gives rise to a foliage leaf, as well as to a floral stalk (Fig. 5 *A*). In this case no foliage leaves are found on the floral stalk which puts forth three or four flowers towards its top. Surrounding the bulb are found numerous bulblets.

Lloydia triflora Bak., from Karuizawa, which flowers in May, is also a small herb, possessing a small bulb with a black cover. The structure of the bulb is the same as that of *Tulipa edulis*, *T. latifolia* and *Gagea japonica*. In the non-flowering plant the outermost sheath elongates into a foliage leaf. In the flowering one also it elongates into a foliage leaf, while the floral stalk is produced from the lateral side of the sheath (Fig. 5 *B*). In other words, this stalk is attached to the outermost sheath of the bulb and not to the stem itself. At the outside of the bulb are found a few bulblets.

A comparison of all the species mentioned above shows that in the non-flowering individuals foliage leaves form the upper parts of the outermost sheaths, while in the flowering ones the mode of attachment of the foliage leaves and floral stalks differs in different species. In *Erythronium* and *Tulipa*, the upper part of the outermost sheath ends as a conical process, while in *Gagea* and *Lloydia* it elongates into a foliage leaf, just as in the non-flowering bulb. The process is, thus, an unfolded leaf. The floral stalk originates near this process in *Erythronium* and *Tulipa*, and near the petiole base in *Gagea*, but in *Lloydia* it goes out from the lateral side of the bulb, and in tulip out of

the basal part of the bulb. The latter is the normal condition in the Liliaceous bulb. If in such a case the lower part of the floral stalk is fused partially with the outermost sheath, a *Lloydia*-like form may be derived, and if the fusion proceeds up to the upper part of the sheath, this will result in a form like *Gagea*. Such a form may be met with also in *Tulipa*, as well as in *Erythronium*. The subterranean organ of *Erythronium japonicum* may thus be interpreted as a bulb, whose sheaths are fused together.

In *Tulipa*, *Gagea* and *Lloydia*, one to five bulblets are produced round the bulb, whose construction is, therefore, more complex. In tulip the base of such a bulblet is attached to the stem base, while in the other species it is attached to the surface of the bulb, being connected to the outer surface of the outermost or inner sheath. Between the place of attachment and the stem base, there is a ridge on the sheath. This suggests that, like the floral stalk, the basal part of the bulblet becomes fused with the sheath. The foliar runner, which emerges from the bulb base in *Tulipa edulis* and *T. latifolia*, differs from the bulblet, and both the runner and the bulblets may be produced in the same individual (Fig. 3*D*, *E*).

In the normal bulb of the Liliaceae the floral stalk may be the main axis. Some buds may be produced between the sheaths, and usually one of these becomes the floral stalk in the following year. Such a sympodial bud formation may be repeated year after year. In *Erythronium*, *Tulipa* and *Gagea*, when we consider the basal part of the floral stalk to be fused with the sheath, this should be the main axis, and a small bud within the bulb the lateral one, though this may appear to be the main bud.

Summary

1. In *Erythronium japonicum*, the subterranean organ is a bulb, whose thickened sheaths fuse with each other to form a common sheath. In the non-flowering individual the upper part of the outermost sheath elongates to form a foliage leaf, and in the flowering one to form a floral stalk.

2. In the allied species, *Tulipa edulis*, *T. latifolia*, *Gagea japonica* and *Lloydia triflora*, the bulb consists of thickened sheaths, which remain separate from each other. In the non-flowering individual, the outermost sheath elongates into a foliage leaf. In the flowering one, it elongates into only a floral stalk in *Tulipa edulis* and *T. latifolia*, or into a foliage leaf and a floral stalk in *Gagea japonica* and *Lloydia triflora*. In the tulip, *Tulipa gesneriana*, the floral stalk arises directly out of the stem base.

3. In the mode of formation of the floral stalk in these species, the typical garden tulip type leads on to the simplest form of *Tulipa* type by a fusion of the stalk with the sheath. This is also the case in *Erythronium japonicum*.

4. In *Tulipa edulis* and *T. latifolia*, as well as in some species of *Tulipa* and *Erythronium* observed by others, a long runner with a small bulb at its tip comes out of the lower part of the bulb by an abnormal elongation of the outermost sheath. The abnormal growth of the base of the bulb of *Erythronium japonicum* is due to the same process, but owing to the fusion of the sheaths the growth is arrested, and the stem base with the basal part of the sheath remains as a small segment. By a repetition of this process a curious appendage may be produced at the base of the bulb.

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FLORAL ANATOMY AND INFERIOR OVARY

V. PURI
Meerut College, Meerut, India

While preparing a review, "The rôle of floral anatomy in the solution of morphological problems", during a recent visit to U.S.A., the author had an opportunity of analysing the literature concerning the nature of inferior ovary. This has led him to think that justice has not been done to the anatomical method in so far as it has often been taken for granted that floral anatomy can invariably solve the problem of the morphological nature of the inferior ovary. Many instances are on record where evidence from vascular anatomy alone has been considered sufficient to uphold one view against the other. The reasoning in many of these cases does not stand critical examination. While the present author holds that as a rule the anatomical method, if used judiciously, can contribute substantially towards a better understanding of many an intricate problem of floral morphology (see Puri, 1951), he thinks that with respect to the problem of the inferior ovary the course and disposition of vascular bundles are not as useful guides as has often been claimed. It is with the object of assessing the real contribution of anatomical studies to the solution of this specific problem that this work has been undertaken.

The morphological nature of the inferior ovary has long remained controversial. The voluminous literature that has accumulated on the subject has been admirably reviewed by Douglas (1944). There seems to be a concensus of opinion that the inner part of the inferior ovary is truly carpellary. The real controversy centres round the nature of the outer part of the 'wall', which has been interpreted by some as appendicular, being formed by the fusion of the bases of the sepals, petals and stamens with the ovary wall, and by others as receptacular, being formed by the fusion of the ovary wall with the wall of the receptacular cup (see Douglas, 1944; Puri, 1951).

In some instances the course and disposition of the vascular bundles do reveal the receptacular nature of the outer region of the 'wall' of the inferior ovary, the stelar tissue typically ascending the wall of the 'floral cup' for some distance. After giving off traces for the peripheral organs, the bundles that are destined to furnish the carpellary traces bend inward and downward. On reaching the bottom of the floral cup they may be wholly consumed in giving off carpellary traces or portions of them may persist as 'residual tissue' of the axis (Smith & Smith, 1942a). It seems to be generally accepted that these bundles which show a 'downturning' in their course are stelar bundles up to about the point they give off carpel-

lary traces and consequently the tissue through which they traverse is receptacular. The ' floral cup ' in such cases, therefore, is receptacular and hence the outer region of the ovary ' wall ' with which it fuses is also receptacular. Such a peculiar course of the stelar bundles, before they give out carpellary traces, has been reported in certain species of the Rosaceae (Jackson, 1934; MacDaniels, 1940), Santalaceae (Smith & Smith, 1942a, 1942b), Cactaceae (Sharma, 1949), Calycanthaceae (Smith, 1928) and some others (for full citations see Douglas, 1944; Puri, 1951). The ' floral cup ' in these cases is believed to have been formed by a process of ' sinking ' or ' invagination ' of the floral axis. How this might have been brought about I have tried to show in Fig. 3A-C. Very early in the development of the flower the growing apex of the floral axis ceases to elongate. Further growth is continued *laterally* in the region of the apex and *vertically* in the peripheral region around it. Consequently the receptacle rises up to a greater or less extent in the form of a hollow cup that carries the peripheral organs on its rim and leaves the carpels at the bottom. This intercalary growth also involves the procambial cylinder which as a result is pushed out, as it were, as a pouch into the wall of the ' floral cup '. On this account the stelar bundles which supply carpellary traces *appear* to descend along the inner wall of the receptacular cup and have the xylem of their bent portions turned abaxially.

Attention should be drawn here to a point of some structural significance which has been brought out in a study of *Darbya* and some other Santalaceae (Smith & Smith, 1942b). Here some of the descending bundles, after they have given off carpellary traces, are said to continue their downward course and disappear ' blindly ' deep into the tissue of the receptacle. They are described as the ' residual bundles ' of the apex of the floral axis. How they have come to point downward is really difficult to understand, unless, of course, we assume with the Smiths that an actual impushing or invagination of the floral axis has taken place. The present author thinks that terms like ' sinking ', ' impushing ', ' invagination ', etc., when used in connection with the floral axis, are just descriptive terms, which are used to describe the peculiar type of differential growth characteristic of certain floral axes. The usage of such terms, therefore, should not involve any idea of an inversion of the floral axis which these authors want us to believe. If the axis in *Darbya* were to become inverted, how could the orientation of the gynaeceum remain unaffected?

In other cases, however, opinion is sharply divided. Some believe that the outer region of the ovary ' wall ' is receptacular, while others hold that it is appendicular. Bugnon (1926, 1928a, 1928b, 1929), who regards the entire ' wall ' as receptacular, has supported his claims on anatomical grounds. Studying the *Begonia* ovary in detail he has reached the conclusion that the vascular bundles traversing the ' wall ' of the ovary are all stelar bundles and consequently the ovary ' wall ' is entirely receptacular. He is definitely against the idea of congenital concrescence which van Tieghem (1871) supported on the basis of the relative distribution of vascular bundles. Langdon (1939) also supported the axial nature of the inferior ovary in the Fagaceae and Juglandaceae on more or less similar grounds. There are many others who have held similar views but they have based them on developmental or ontogenetic studies and as such a consideration of these is outside the scope of this paper.

The appendicular view was admirably advocated by van Tieghem (1871) and after him by Eames, who is perhaps its strongest exponent at present. On the basis of his anatomical studies Eames (1931) has asserted that " the inferior ovary in all or nearly all families has resulted from the adnation of the outer floral whorls to the carpels. Histological evidence of this is available but abundant proof is supplied by the course of the bundles and the manner of their forking and splitting. " Gauthier (1950), who worked on the *Begonia* ovary, has emphatically refuted the claims of Bugnon that the bundles in the ovary ' wall ' are stelar bundles. Indeed Gauthier has shown beyond any reasonable

doubt that the bundles in question are really foliar bundles meant for the different floral organs, and that there is no question of the existence of an anatomical node in the 'floral cup', as Bugnon (1926) would want us to believe.

Recently MacDaniels (1940) has presented the case of the appendicular view while dealing with the so often controverted pome fruit of the Rosaceae. Both Eames and MacDaniels have given particularly instructive series of diagrams from the Ericaceae and Rosaceae respectively to show how by simple adnation and cohesion of the basal regions of the sepals, petals and stamens with the ovary wall the superior ovary can become inferior. Others who have held a similar opinion include Smith and Smith (1942a, 1942b), Swamy (1948), Gauthier (1950), Eames and MacDaniels (1947), Rao (1949), Wilkinson (1949), etc.

The difference between Bugnon on the one hand and Eames and his supporters on the other resolves into this: while the former considers the bundles in the ovary 'wall' as stelar, the latter interpret them as appendicular. The point at issue between floral anatomists, therefore, seems to have been whether the bundles in the ovary 'wall' are axial or appendicular. The present author is inclined to believe that this is no longer a problem. The work of Eames (1931) and Gauthier (1950) has shown beyond doubt that these bundles are, as a rule, appendicular. The solution of this problem has led some to believe that this is also the key to the solution of the problem of the inferior ovary. Such is, however, not the case, for we know that leaf traces may arise in stems at a considerable distance below the level of the leaf, in tissues which are clearly not leaf tissues.

The nature of the inferior ovary is, in my opinion, a part of that ever-insoluble (?) problem as to where the axis ends and the leaf begins. We cannot help stating here that modern studies have deprived the terms 'axis' and 'leaf' of much of their morphological significance (see Arber, 1950). They are now merely descriptive terms which serve for convenience more than any thing else. The problem of the inferior ovary, therefore, loses much of the importance that was attached to it in the past; and consequently the brief discussion that follows is primarily from the standpoint of description. The present author no longer regards it as of any vital significance.

Let us, for the time being, agree with Eames that the inferior ovary is always appendicular. Such a situation would involve one or the other of the following assumptions: either (1) there is no receptacular cortex in the region of the floral appendages, or (2) if the cortex is present, the growth which brings about the inferior position of the ovary is confined to its extreme peripheral region adjoining the bases of sepals, petals and stamens and never involves the internal or deeper layers.

The first of these assumptions is clearly involved in the so-called principle advanced by van Tieghem (1871) that "the differentiation of a floral part begins at the point where the vascular supply leaves the stele". A necessary corollary of this will be that the vascular bundles, as soon as they separate from the parent stele, begin to traverse the tissue of the organ for which they are intended, that is, there is no cortical tissue between the floral appendage and the stele of the receptacle. MacDaniels (1940) has held such a consideration as valid and makes this the basis for supporting the appendicular view.

The present author, however, thinks differently. While admitting that the exact location of the differentiation of a floral part can but be indicated arbitrarily, he believes that an acceptance of van Tieghem's view would land us in serious difficulties. Not only is it against our conception of an exogenous origin of floral organs and our general notions about the structure of the receptacle, but it is also contrary to the evidence from recent work on development and histogenesis. Overwhelming data have accumulated which go to show that floral organs, like foliage leaves, are initiated by periclinal divisions in the peripheral layers (tunica) of the axis. This point has been made especially clear in the case of the foliage leaf. In wheat there is only a one-layered tunica and the leaf

with its procambium differentiates from this layer (Rösler, 1928). Summing up the condition in the dicotyledons, Gifford (1951) writes: " beginning of leaf initiation is generally in the second layer, irrespective of the number of tunica layers ". In *Vinca rosea* the stamens and the carpels are initiated in the second layer of the tunica (Boke, 1949) and sepals and petals from the second and third (Boke, 1948). In many of the Compositae, the leaves, bracts and floral organs are all derived from the second layer of tunica (Lawalree, 1948). Gregoire (1931, 1935, 1938), who considers the receptacle as fundamentally different from a vegetative shoot, attributes the anatomical differences noticed by him in the two cases to the condition that in contrast to true leaves all floral organs arise from a superficial and shallow meristem, i.e. the ' embryonic muff '. Numerous other instances of this type, particularly those dealing with foliage leaves, are on record (see Esau, 1943; Sifton, 1944; Philipson, 1949). In the face of these observations it is no longer possible for us to believe in the out-of-date statement of van Tieghem, much less to base our conclusions on that.

As far as the present author could determine there is no statement worth our notice, on record, where the floral leaves are shown to be initiated in deeper layers where the procambium differentiates. Some work has, however, been done on the differentiation of foliage leaves which goes to show that leaf traces determine the leaf (Crafts, 1943; Esau, 1943; Gunckel & Wetmore, 1946a, 1946b; Priestley & Scott, 1936; Sterling, 1945). This inference, which is based on the observation that in these cases the traces are formed before the leaves, is controverted for *Lupinus albus* (Snow & Snow, 1947); but even if it is taken for granted that it is generally so, we have yet to distinguish between *what* determines a leaf and *where* a leaf actually differentiates.

Wardlaw's recent work on morphogenesis, on the other hand, indicates that traces for organs differentiate as a result of the basipetal movement of metabolites from the active apices of these organs. In *Primula* and certain ferns he could experimentally prevent the formation of a trace from the stele by removing the leaf primordium at a very early stage (see Wardlaw, 1950; and literature cited therein).

Further, it has been claimed that the procambium in the developing carpels of *Amygdalus* appears first in the central part of the primordium and only afterwards becomes connected with the vascular system of the receptacle by basipetal extension (Brooks, 1940). Such a condition is reported to be quite common in angiosperm leaves (Nast, 1944; Philipson, 1949; Sifton, 1944; Gregoire, 1938). If this, as seems likely, turns out to be a more general condition, it will deal another serious blow to van Tieghem's conception.

From all these considerations we may conclude that floral organs always differentiate from the peripheral layers, an exact definition of whose limits is neither possible nor relevant to our consideration here; and that some amount of cortical tissue always exists between the stele of the receptacle and floral primordia. Morphologists, in general, do not seem to question such an inference for they often speak of a receptacular cortex (see Eames, 1931; Wilson & Just, 1939). This cortical tissue has to be traversed before a bundle can enter its organ. In fact the term ' trace ' is used to denote this feature; it is a ' trace ' as long as it remains in the cortex and becomes a ' bundle ' the moment it enters the tissue of its organ. It is quite obvious, therefore, that MacDaniels (1940) is not justified in basing his conclusions on van Tieghem's erroneous concept of the receptacle.

Likewise, the second assumption too cannot stand critical examination, for it is difficult, if not impossible, to prove that the growth which brings about the inferior position of the ovary is confined to extreme peripheral layers. In fact it may as well take place in deeper and inner layers of the receptacle. In the gamocondition of the calyx, corolla and androecium each whorl grows independently of the other. It is not likely, therefore, that meristematic activity extends to deeper layers; for if it were so, the corolla would not be separate from the andro-

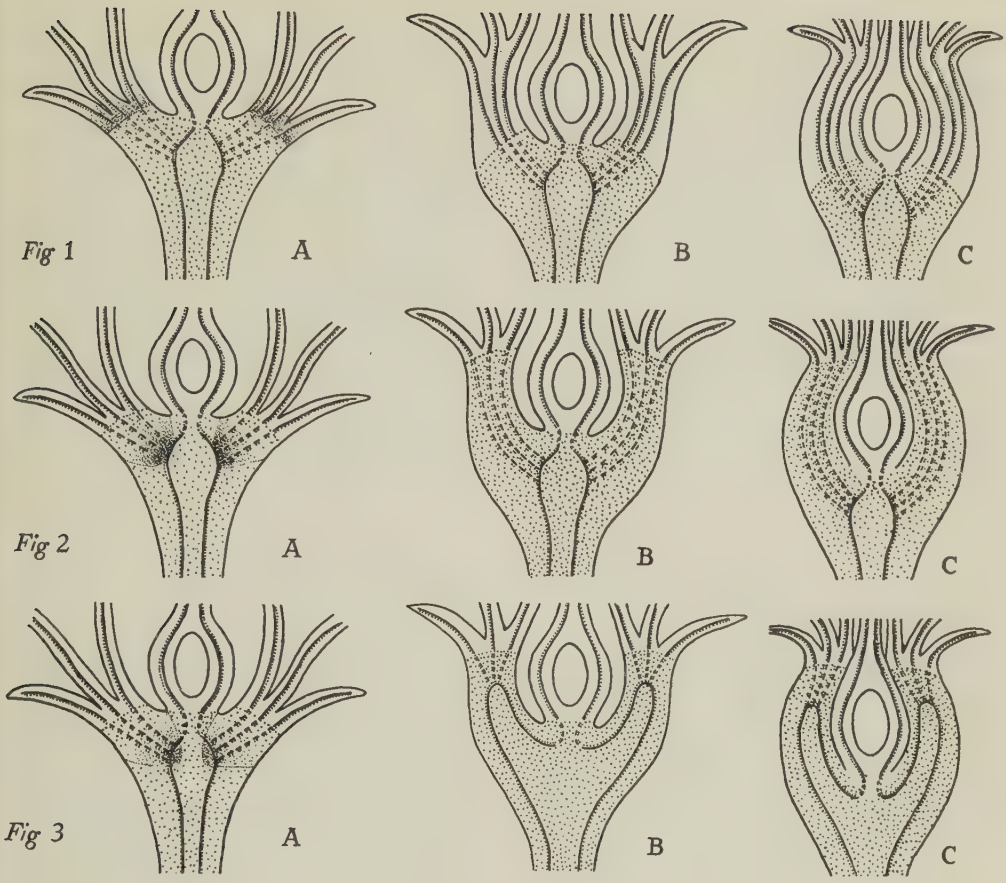
ecium and the calyx[1]. Again, when stamens are epipetalous, meristematic activity may not extend to much deeper layers for calyx is still free from the corolla tube. This type of zonal growth which is restricted to the peripheral region only may be termed respectively as 'cohesion' and 'adnation'. For growth involving deeper layers, it is obvious that these terms will not be appropriate; mere 'zonal growth' may be better.

In the case of the inferior ovary, however, the condition is quite different. Here we have no reason to believe that meristematic activity does not involve the deeper and more internal layers of the receptacle, since all floral parts 'grow' together. Excessive zonal growth in these internal layers, through which traces have to pass before entering organs, may take the floral organs on to the top of the ovary. Obviously, therefore, the nature of the 'floral cup' or the 'ovary wall' will vary with the region which is most active in zonal growth. There appear to be at least three possibilities with regard to this zonal growth: (1) It may be most active in the extreme peripheral region of the receptacle, involving for the chief part only the bases of the floral organs. (2) It may be most active in the middle layers, just outside the region where 'procambium' tissue differentiates. (3) Or, in extreme cases, it may be most active on the inner side of the region where 'procambium' tissue differentiates.

The three conditions are represented diagrammatically in Figs. 1-3. It is generally believed that the first condition will result in more or less appendicular 'floral cup' as is usually the case in the gamopetalous corolla. Similarly there can be little doubt that in the third case the resulting outgrowth will be mainly receptacular as has been shown to be the case in *Calycanthus* (Smith, 1928), *Rosa* (Jackson, 1934), *Pereskia* (Sharma, 1949), certain species of the Santalaceae (Smith & Smith, 1942a, 1942b; Schaeppi, 1942; Schaeppi & Steindl, 1937; Fagerlind, 1948) and others. These two conditions are well recognized, but unfortunately the second condition (Fig. 2), which is intermediate between them, has not been even conceived of so far. It was perhaps lack of appreciation of this possibility which led MacDaniels (1940, p. 20) to argue that "if the pome flowers were in part receptacular in nature a doubling back of the stelar bundles, supplying the carpels would be expected as is the case with *Rosa* and with *Rubus odoratus*". A reference to Fig. 2 will convince anybody that even without the stelar tissue being involved in zonal growth, the 'floral cup' can still be partly receptacular and partly appendicular, depending upon how much the inner cortex or the outer peripheral layers of the receptacle grow. If the former is more active, the 'floral cup' will be mostly receptacular and if the latter grows more than the former, it will be mostly appendicular. That such differential zonal growth, which may not involve the vascular cylinder but only the cortex of the receptacle is within the range of possibility seems to be indicated by the occurrence of receptacular discs which do not have any bulging of stelar tissue, e.g. in *Crataeva religiosa* (Puri, 1950).

The 'floral cup' which forms the outer wall of the ovary will, therefore, be mostly appendicular in Fig. 1 and receptacular in Figs. 2 and 3. Now, with regard to our main problem, it is obvious that in Figs. 1 and 2 the vascular ground plan will be practically the same and it will be very difficult, if not impossible, to distinguish between the receptacular and appendicular 'cup' merely on the basis of anatomy. It is true that in both these cases the vascular bundles are appendicular, rather than stelar. But, as has already been pointed out (Puri, 1951), it must be remembered that an appendicular bundle has a dual character: *it is a 'trace' when it traverses the cortex of the receptacle and 'bundle' when it enters the organ.* Now, we have no easy means of distinguishing where one ends and the other begins. Hence vascular anatomy can help us little in solving the problem of the inferior ovary in cases similar to those shown in Figs. 1

1. Boke (1948) has, however, concluded that the basal part of the gamopetalous corolla in *Vinca rosea* is receptacular.



FIGS. 1-3 — Schematic representation of the three possible ways in which an inferior ovary can originate. The dotted regions represent the receptacle while the more densely dotted areas in A indicate the centres of most active growth; broken lines represent the ' trace ' parts of vascular bundles and dotted lines the phloem.

and 2. Detailed histogenetic and cytological studies of the receptacle may perhaps yield more reliable evidence. The recent works of Blaser and Einset (1950) and Gifford (1951) have, probably, opened new approaches to the problem.

Summary

The morphological nature of the " wall " of the inferior ovary has long remained a controversial problem. While most authors seem to agree on interpreting the internal region as truly carpellary, opinion is sharply divided as to the nature of the outer region of the ' wall '. Some of the authors describe it as ' foliar ' while others interpret it as ' axial '. Evidence from different fields of study has been brought forward to support one view against the other. During recent years the course and disposition of vascular bundles in the ovary wall have also been called upon, as it were, to support the ' foliar ' view. A critical examination of the recent literature on this aspect of the subject has revealed to the author that in majority of cases the evidence brought forward by floral anatomists in support

of the 'foliar' view is not convincing. In fact the present author is inclined to believe that the anatomical method in general is of little use in solving the problem of the inferior ovary. We have to look to some other fields of study for the solution of the problem if it still exists.

The author is indebted to the numerous friends in U.S.A. and Europe with whom he had the privilege of discussing the problem during his recent tour abroad. While not claiming their support for the views expressed in this paper, he has great pleasure in recording his sincere thanks to all of them, especially Professors A. J. Eames and L. H. MacDaniels, Dr. H. P. Banks and Dr. C. Burch (Cornell Univ.); Professors I. W. Bailey and R. H. Wetmore (Harvard Univ.); Dr. Th. Just (Chicago Natural Hist. Museum); Miss B. Palser (Univ. of Chicago); Miss E. L. Fisk (Univ. of Wisconsin); the late Prof. J. T. Buchholz and Prof. O. Tippo (Univ. of Illinois); Prof. A. S. Foster (Univ. of California); Prof. Dr. Hans Weber (Univ. of Mainz), Drs. W. Leinfellner and F. Ehrendorfer (Univ. of Vienna); Prof. P. Maheshwari (Univ. of Delhi); and to Prof. C. W. Wardlaw (Univ. of Manchester), who has also gone through the manuscript and made valuable suggestions. To the Government of Uttar Pradesh the author is indebted for some financial and technical assistance.

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THE STAMENS OF RICINUS

L. VAN DER PIJL
Department of Botany, University of Indonesia, Bandung, Indonesia

Since Zimmermann used the stamens of *Ricinus communis* to apply his " Telome theory " to higher plants, this plant has entered handbooks as a standard proof of the " New Morphology ". The " telomists " attempt to demonstrate the origin of higher plants with stems, leaves and roots from lower plants (Psilophytales) having a dichotomously branched thallus. The terminal branchlets that may produce spores are called telomes.

According to this theory (Zimmermann, 1938) the branched staminal bundles of *Ricinus* are of special significance, because (a) they resemble the sporangiophores (axial organs with sporangia) of some fossil vascular plants; (b) they show a perfect dichotomous branching; and (c) the sporangia (thecae) are not lateral organs like those borne on classical sporophylls, but are the terminal structures as postulated by the telome theory.

To an unbiassed observer it may seem strange that so highly developed a plant as *Ricinus* should show a complete regression to a very primitive condition. It is even more astonishing in view of the fact that other Euphorbiaceae have microsporophylls of the usual type. Further, although the family shows a reduction in the organization of the individual flower, there is also seen a tendency towards their aggregation into complex inflorescences. These inflorescences, the cyathia, show a strong resemblance to flowers. In the light of this, one might think of interpreting the branched staminal bundles of *Ricinus* as secondary structures, i.e. contractions of dichasial male inflorescences. However, as far as I know, nobody has expressed such a view and I see no reason to support the idea.

A fourth peculiarity in the stamens of *Ricinus*, which gives them a pseudo-primitive character and which has been exploited by " telomists ", is that the thecae have a one-layered wall, that the mechanism for dehiscence lies in the epidermis (both characters also found in ferns) and that the cohesion mechanism also works as in ferns — at first a slow opening, then a sudden rebound to the original position, whereby the spores are scattered in the wind (see Steinbrinck, 1910).

Considerations concerning the dichotomy in these stamens seem to be based largely on an old figure from Sachs' Lehrbuch (1873), which has been frequently reproduced in other books. According to the old morphology it shows the filaments and anthers multiplied by repeated branching of the primordia. At the top the two thecae are also shown to be separated by a deep cleft. Telomists, on the other hand, explain it as a dichotomous system of sporangiophores.

Recently Lam (1948) has once again referred to the case of *Ricinus*. Part of the old drawing has been reproduced by him on p. 142 (redrawn here as Fig. 1) as representing a typical case of " stachyospory " (sporangia on axial segments) in seed-plants in contrast to the " phyllospory " of orthodox carpels derived from one like that of *Cycas*. He also mentions and figures (p. 119) the presence of a lateral organ at the side of some of the ultimate ramifications and regards it as an angular leaf at the fork — one more primitive character.

My investigation of *Ricinus communis* in Java has, however, shown that this view is quite incorrect. In microtome sections of young male flowers I found perfectly normal anthers with four loculi in two thecae, occurring in one plane and united by a connective. Mature stamens

FIG. 1 — Staminal bundle of *Ricinus communis* (copied from Sachs' Lehrbuch, 1873). FIGS. 2, 3 — Ends of staminal bundles of two varieties of *Ricinus communis* from Java.

from open flowers showed the same condition (Fig. 3). The two thecae have a deep incision between them but the connective protrudes between the two as a transparent, glassy point. In one variety the two thecae could be said to be situated on top of a fork but here too the protrusion of the connective was always present. Though Lam (1948) himself gives clear figures of the anthers with a protruded connective (see his Fig. 6), it is surprising that this organ was not found by other botanists. One might, however, admit the existence of varieties with a greater separation of the thecae. Perhaps also the protrusion shrivels in dry air and poorly fixed material. The "angular leaf" of Lam is no doubt nothing other than the point of the connective.

My observations further show that the microsporangia are not placed terminally, but laterally. This speaks against stachyospory and for phyllospory (cf. Parkin, 1951). It may, therefore, be stated quite definitely that *Ricinus* gives no evidence whatever of telomy in seed plants!

I shall merely add a few more words about the other supposed pteridophytic character, regarding structure and behaviour of the wall of the microsporangium. The one-layered condition, on further study, proved to be a secondary reduction, and is not the original condition at all. Until the beginning of the reduction division the wall comprises no less than three layers of cells outside the tapetum. When the microspore mother cells begin to round up, the cells of the innermost layer of the wall begin to collapse. As the cells of the hypodermal layer are the largest, it seems likely that it is this layer which persists at maturity and becomes the fibrous layer. In that case the occurrence of a normal endothecium is established.

Staedtler (1923) has also called attention to the reduction in the wall of the anther in explosive anthers. He also illustrates (see his Fig. 8) the remnants of the epidermal cells outside the fibrous layer in the mature anthers of *Ricinus* and the initial three-layered condition of the wall (see his Fig. 9).

I can confirm the explosive discharge of the pollen grains. The initial slow dehiscing can be speeded up by bringing a hot needle near the anther or putting the flower in sunshine. Whether it is indeed a cohesion process with the final intrusion of a gas bubble I am unable to decide. There is nothing surprising about the final rebound in *Ricinus*, but rather about its absence in ordinary anthers. The explosion depends on the removal of a brake mechanism, present in ordinary anthers and perhaps situated in the epidermis, which is lacking here.

The diverse contrivances in the anthers are not any indications of primitivity but new adaptations developed in connection with a new mode of pollination. *Ricinus communis* has probably changed rather recently from entomophily to anemophily. The amount of pollen and number of anthers has been augmented and the mode of dehiscence adapted to the dispersal of pollen by wind. Other anemophilous plants have developed a different kind of dehiscence mechanism.

Pohl (1929) demonstrated the presence of "*Pollenkitt*" in *Ricinus*. This means that its anemophily is a secondary phenomenon.

Even now the connection with insects has not disappeared entirely. There are small extrafloral nectaries between the flowers and these are visited by wasps like *Sceliphron violaceum*. In doing this the wasps run over the anthers and stigmas and bring about pollination.

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PLACENTATION IN PEPEROMIA

Y. S. MURTY

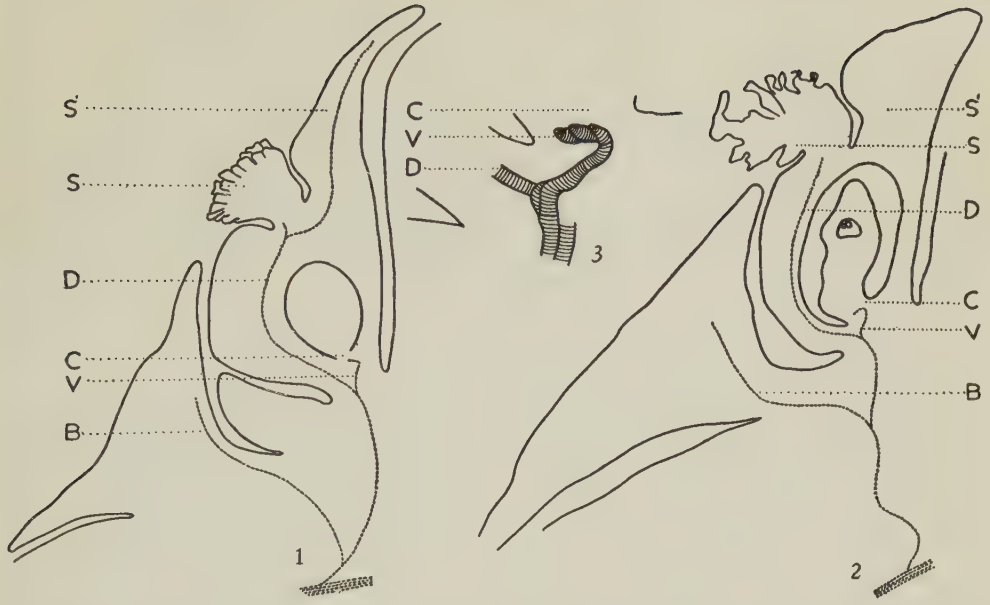
Meerut College, Meerut, India

Information on certain aspects of the morphology of the Piperaceae is still meagre or wanting and conflicting opinions have been expressed regarding such subjects as the past history of the family, placentation, nature of the ovule, etc. During his recent tour abroad, Dr. V. Puri collected material of certain species of *Peperomia* from the Cornell University, Ithaca; Bergianska Botanical Garden, Stockholm; and the Botanical Garden, Kiel, and gave it to me for study. In addition I was able to collect some species from South India.

So far about 18 species have been examined from the point of view of floral anatomy and embryology. As the study has yielded some interesting results, particularly with respect to placentation, and as the full account will not be ready before long, it is considered worth while to publish some of these results in the form of a short note.

The inflorescence is an unbranched spike. The flowers, which are partially sunk in the inflorescence axis, are naked and each is subtended by a shield-like bract which protects it in the early stages (Figs. 1, 2). There are two laterally placed stamens, each with a bilocular anther. The sessile or sub-sessile gynaeceum is unilocular with a single orthotropous ovule. It is crowned by two more or less unequal outgrowths. That on the anterior side is the small papillate receptive lobe of the stigma while the other on the posterior side is the non-receptive lobe (Figs. 1, 2).

Each flower receives a single vascular strand which diverges from the stele of the inflorescence axis a little below the level of origin of the flower. Before entering the flower it gives off a small branch for the bract (Fig. 1B). A little higher up in the pedicel it gives off two more branches, right and left, for the two stamens (not shown in the figures). The remaining strand enters the base of the ovary and divides into two. The anterior branch, which is always more prominent than the other, continues up into the anterior (abaxial) side of the ovary wall (Figs. 1, 2D). In some species, namely *P. incana*, *P. cniapas*, *P. blanda* and *P. fenzlei*, this enters directly into the base of the receptive lobe of the stigma while in others a more or less prominent branch may be given out towards the non-receptive lobe. The behaviour of this branch, however, is very variable in differ-



FIGS. 1-3 — Fig. 1, l.s. flower of *Peperomia argyreia*. × 82. Fig. 2, l.s. flower of *Peperomia cniapas*. × 117. Fig. 3, vascular supply to the ovule in *P. cniapas*. × 333. (B, vascular supply to the bract; C, chalaza; D, dorsal bundle; V, ventral bundle; S, receptive part of stigma; S′, non-receptive part of stigma).

ent species. In *P. argyreia* (Fig. 1) it continues right up to the tip of the non-receptive lobe on the adaxial side. In *P. prostrata* it disappears about the middle of the lobe. In *P. pellucida* and *P. sandersii* this spreads more or less horizontally and forms a lattice work of tracheides at the top of the ovary, while in *P. reflexa* and *P. randiflora* only a few tracheides go to form this horizontal plate.

The other vascular branch in the base of the ovary may ascend vertically towards the chalazal region of the ovule, as in *P. pellucida, P. incana,* etc., or it may adopt a more or less oblique course. In a few species like *P. cniapas* (Figs. 2, 3V), *P. argyreia* (Fig. 1V) and *P. blanda,* this bundle ascends obliquely towards the posterior side for a short distance, then curves abaxially again towards the base of the chalaza. In certain other species (e.g. *P. reflexa* and occasionally *P. argyreia*), although the curvature in the course of this bundle is not so marked, the tracheides, particularly in its upper region, are horizontally oriented showing again some compression or reduction in their course.

It is generally believed that the single ovule in the Piperaceae springs from the base of the ovary, and that it is terminal. Not only the ovule as a whole but also the nucellus is regarded as an axial structure.

The present study does not support such an interpretation but shows clearly that the ovule is carpellary and really lateral in position, and that the apparently basal position is derived. In *P. cniapas* the ventral bundle takes a curve from the posterior side of the ovary wall and then approaches the chalaza. This curving of the vascular bundle is considered here as an important structural feature for it foils any attempt to interpret the ovule of *Peperomia* as basal or axial and indicates clearly that it is brought down to the basal position during phylogeny. This is very similar to the condition in *Boehmeria cylindrica,* where also the apparently basal position of the ovule is really a derived one (Bechtel, 1921).

Summary and Conclusion

It is concluded that the ancestors of *Peperomia* had parietal placentae and that the apparently basal position is a derived one. Even for description the term "basal" is not appropriate in this case for this type of placentation is derived from the axile or free central type (cf. Puri, 1952). The condition in *Peperomia* is best described as sub-basal, a term once employed by Baillon (1874).

It is a pleasure for me to record my grateful thanks to Dr. V. Puri for his unfailing interest in the progress of the work and for much helpful guidance. I am also thankful to Prof. P. Maheshwari for his valuable suggestions and for the loan of some literature from his personal library.

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THE MORPHOLOGY AND BIOLOGY OF SOME PRIMITIVE ORCHID FLOWERS

O. HAGERUP

Botanical Museum, University of Copenhagen, Denmark

Introduction

Few botanical objects have attracted so much attention from either the botanist or the layman as the phantastic flowers of the orchids. A very extensive literature has grown on this subject but much still remains to be done. This applies even to the fundamental features of the structure of the flower, although they were so carefully examined by the great morphologists of the last century, whose main results are embodied in Eichler's classic diagrams which have found a well-deserved place in all handbooks of botany.

According to the classical view, the orchid flower is derived from the ordinary trimerous, monocotylous type like that of *Tulipa* in which the androecium is composed of two triandrous whorls each consisting of three stamens. In most orchids only one of these persists (Fig. 9, *a*), while the five remaining ones (Fig. 9, *b-f*) are either partially or wholly suppressed.

From a study of a few small-flowered specimens I have found some structural features which had hitherto remained unnoticed but which in some ways throw a new light on the morphology and biology of the orchid flower. These plants had, no doubt, already been investigated by the morphologists and biologists of the last century, but owing to technical difficulties and their small size they could not be studied with such thoroughness as can be done now with the aid of microtome sections.

Herminium monorchis was the most interesting of all the small-flowered species

examined by me. Living flowers in all stages of development were available and were examined directly as well as from serial sections. All the figures drawn here are so arranged that the labellum is turned downwards (in front) and the anther upwards (at back). Concerning the general structure of the flower of orchids and its interpretations a reference may be made to Vermeulen (1947).

Observations

Androecium — If the perianth is removed from a fully opened flower of *Herminium* (Fig. 1), we find an androecium (Fig. 2) which so closely resembles that of the well-known *Orchis* (Fig. 7) that the corresponding individual organs may easily be homologized in the following way:

Fig. 2 shows the ordinary anther (*a*) which is the median member of the outermost whorl of the androecium; to the right and left of this are the two auriculae (*d*, *e*) which represent the two rudimentary stamens of the inner whorl. These appear as glands, and perhaps they are the organs which give fragrance to the flower.

Directly below the two halves of the anther there are seen the two peculiar structures called bursiculae (*b*, *c*). In *Orchis* (Fig. 7) they are insignificant little swellings on the rostellum which appear to be parts of the latter, but in *Herminium* (Fig. 2) they are well developed and must be regarded as independent organs of remarkable form and size without any connection either with the anther or with the other co-ordinate organs.

When first initiated, the bursiculae appear as two isolated half-moons (Fig. 3, *b*, *c*), which are situated on the right and left of the rostellum (A), but without any connection with the latter. Not until the further development of the flower do the bursiculae and the anther fuse to form the viscid discs of the latter. However, even in the fully developed flower there is no reason to regard the bursiculae as part of the rostellum, as was done formerly — among other reasons probably because this seems to be the condition in *Orchis* (Fig. 7).

In *Orchis* it is only a part of the interior of the bursiculae that forms the viscid disc, but in *Herminium* entire bursiculae (Fig. 5) are removed, when an insect pollinates the flower.

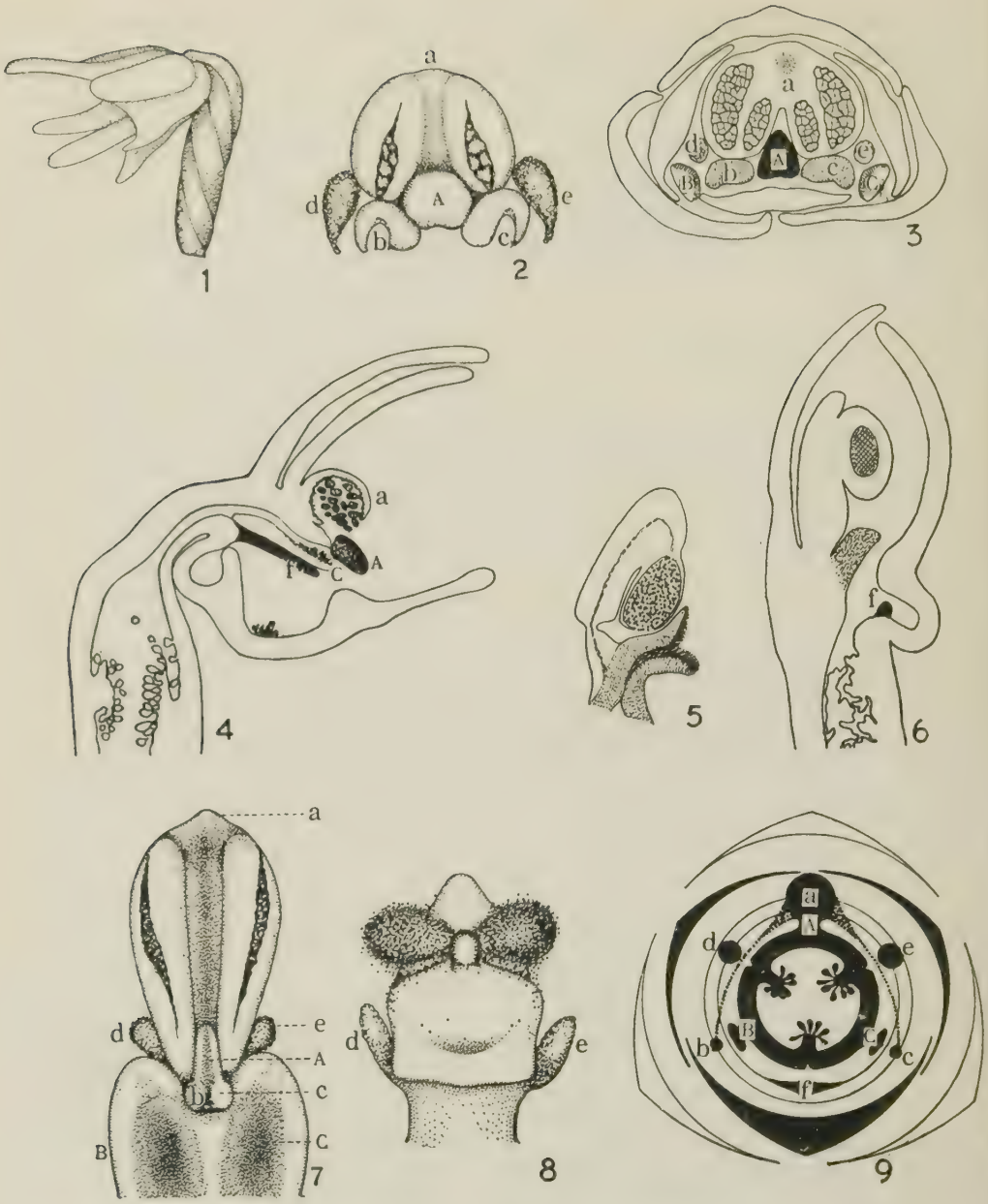
According to the place and the manner in which they are constructed, the bursiculae (Figs. 2,3,7, *b*, *c*) seem to represent the two co-ordinate stamens of the outer whorl, which has thus *not* completely disappeared as is generally supposed to be the case in the majority of the orchids. They have instead become a link in the peculiar mode of pollination of the flower.

In the *Herminium* flower there are thus typically at least 5 stamens which prompt one to look for the sixth member. If this actually exists, it must lie in front at the entrance of the spur so that a median longitudinal section would be the most suitable for demonstrating it. Here (Fig. 4, *f*) it is actually found as a scaly rudiment growing together with the styles (Fig. 4, *C*).

In *Coeloglossum* (= *Habenaria*) *viride* (Fig. 6) the sixth stamen (shown solid black in the figure) is found as a broad, thin membrane, covering the entrance of the spur and it has to be penetrated by the insect which visits the flower for nectar. It is also found, although in a more rudimentary condition in *Spiranthes spiralis* and *Habenaria hyperborea*, but is absent in *Orchis* and *Chamaeorchis*. How common this organ is in other orchids can only be decided by future investigations. Eichler (1875, p. 181) also records it for a few Australian genera, viz. *Glossodia*.

The two staminodes (Figs. 2, 3, 7, *b*, *c*), from which the viscid discs arise, are probably found in all members of the Bastionae and perhaps also in some Acrotonae.

Gynoecium — In *Herminium* the 3 styles are just as remarkable as the stamens. In most orchids there are two functional stigmas, which are broad, disc-like and sessile (Fig. 7, *B*, *C*), while the third and median style situated at the back is converted into the so-called rostellum (Fig. 7, *A*), whose apex is transformed



FIGS. 1-9 — Fig. 1, *Herminium monorchis*, open flower. × 13. Fig. 2, gynostemium as seen from front (*A*, rostellum or viscid body; *a*, anther; *b* and *c*, bursiculae; *d* and *e*, auriculae). × 33. Fig. 3, transverse section of bud (*A*, *B* and *C*, styles; *a*, fertile anther; *b* and *c*, bursiculae or staminodes of outer whorl; *d* and *e*, auriculae or staminodes of inner whorl. × 33. Fig. 4, open flower in l.s. showing autogamy (*A*, rostellum with viscid body; *C*, style pollinated with own pollen; *a*, fertile anther; *f*, sixth stamen or staminode from inner whorl). × 27. Fig. 5, *Epipactis purpurata*, l.s. of gynostemium showing stigmatic papillae on rostellum. × 12. Fig. 6, *Coeloglossum viride*, l.s of bud, showing at *f* the sixth stamen or staminodium. 27 ×. Fig. 7, *Orchis maculatus*, gynostemium (*A*, fold of rostellum; *B* and *C*, stigma; *a*, anther; *b* and *c*, bursiculae or staminodes of outer whorl; *d* and *e*, auriculae or staminodes from inner whorl). × 18. Fig. 8, *Epipactis dunensis*, gynostemium showing autogamy (*d* and *e*, auriculae). × 12. Fig. 9, revised floral diagram of the orchid flower (*A*, rostellum, generally sterile; *B* and *C*, fertile stigmas; *a*, anther of outer whorl which is fertile in Monandria; *b* and *c*, the bursiculae or staminodes of the outer whorl; *d* and *e*, auriculae or staminodes of inner whorl which are fertile in Diandria; *f*, sixth stamen represented as a staminode in *Herminium* and *Coeloglossum*.

into a viscid body in the acrotonous orchids, while the rest of the rostellum has no stigmatic papillae and is incapable of functioning as a stigma.

In *Herminium* the styles are quite different. The two co-ordinate functioning stigmas are thread-like (Fig. 4, *C*) and easily seen in a transverse section (Fig. 3, *B* & *C*). This primitive form of the style is very rare in orchids but it is of much biological significance in autogamy.

The rostellum is best studied in a longitudinal section of the flower (Fig. 4, *A*). Its upper part is transformed into a viscid body which is so conspicuous that this alone is visible when the style is seen from the front (Fig. 2, *A*). This large structure is thrown off during insect visits, because it is attached only by a very thin stalk. After pollination only the basal part of the rostellum is left which probably explains why this organ was missed by earlier workers. However, the incorrect illustrations of those days are still repeated in modern manuals. Attention had not been paid to the remarkable fact that *Herminium* is both bastionous and acrotonous at the same time, a phenomenon which is probably unknown in any other orchid.

Pollination—Darwin had already observed that insect visits are abundant and this has been confirmed by several other investigators (Knuth, 1899, p. 443).

However, if insect visits fail, the flower pollinates itself. After the open flower has reached a certain age, the pollen masses loosen from one another in small lumps or massulae. When the plant is shaken by wind, the pollen falls down from the anther along the sides of rostellum, inevitably hitting the stigmas at the top of the long styles (Fig. 4). This kind of autogamy is so effective that nearly all flowers are pollinated, even if they are cut away and put under glass or in a room. Almost all our native, small orchids pollinate themselves similarly (Hagerup, 1952), which enables them to exist in northern localities where the insect population is small. Some of them bear stigmatic papillae on the rostellum (Fig. 5), a device which greatly facilitates autogamy. As examples may be mentioned, *Habenaria hyperborea*, *Spiranthes*, *Cephalanthera* and *Epipactis*.

Taxonomy — From the above it is clear that *Herminium* is an interesting link between the two, otherwise sharply separated groups, Bastionae and Acrotonae, to which the majority of the orchids (*Monandria*) belong. The question arises as to in which of these groups should *Herminium* be placed.

From a purely morphological viewpoint one would expect to find the nearest relations of *Herminium* among the Acrotonae. The decisive characters lie in the structure of the rostellum. In Pfitzer's (1889, p. 114) keys, for instance, we find *Herminium* placed in the group Physureae, to which also belong *Goodyera* and other genera. Under this group there also exist *Vrydagzynea* and *Macodes* with curious scales in the place where the sixth stamen may be expected to be found as a rudiment.

Figs. 2 and 3 show that the pollen masses are found quite near the two different kinds of viscid organs, so that it is as easy to fancy a connection with the rostellum (*A*) as with the bursiculae (*b*, *c*). As it is, however, the pollen masses actually become attached to the bursiculae so that it is probably correct to place *Herminium* under the Bastionae near *Platanthera* or *Habenaria*.

Summary

The morphology of the flower of *Herminium monorchis* was examined and the results have been diagrammatized in Fig. 9. Contrary to the usual view, the bursiculae are not parts of the rostellum but independent organs representing rudimentary stamens belonging to the outer whorl and joining below with the rostellum. These are the organs which form the viscid discs or retinacula. The upper half of the rostellum is transformed into an adhesive gland (Fig. 4, *A*) just as in the Acrotonae. The flower can be pollinated by insects, but autogamy also occurs, the massulae separating and falling upon the elongated styles (Figs. 4 & 6, *f*). Between the styles is

present a scaly rudiment (Figs. 3 & 4, *B*, *C*) which represents the sixth stamen. *Herminium* is thus an interesting connecting link between the Bastionae and Acrotonae. This one and *Coeloglossum* (Fig. 6) are probably the only ones among orchids in which six stamens have been demonstrated.

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THE GAMETOPHYTE AND YOUNG SPOROPHYTE OF *MATONIA PECTINATA* R. BR.

ALMA G. STOKEY AND LENETTE R. ATKINSON

Mount Holyoke College, South Hadley, Mass., U.S.A. and Amherst, Mass., U.S.A.

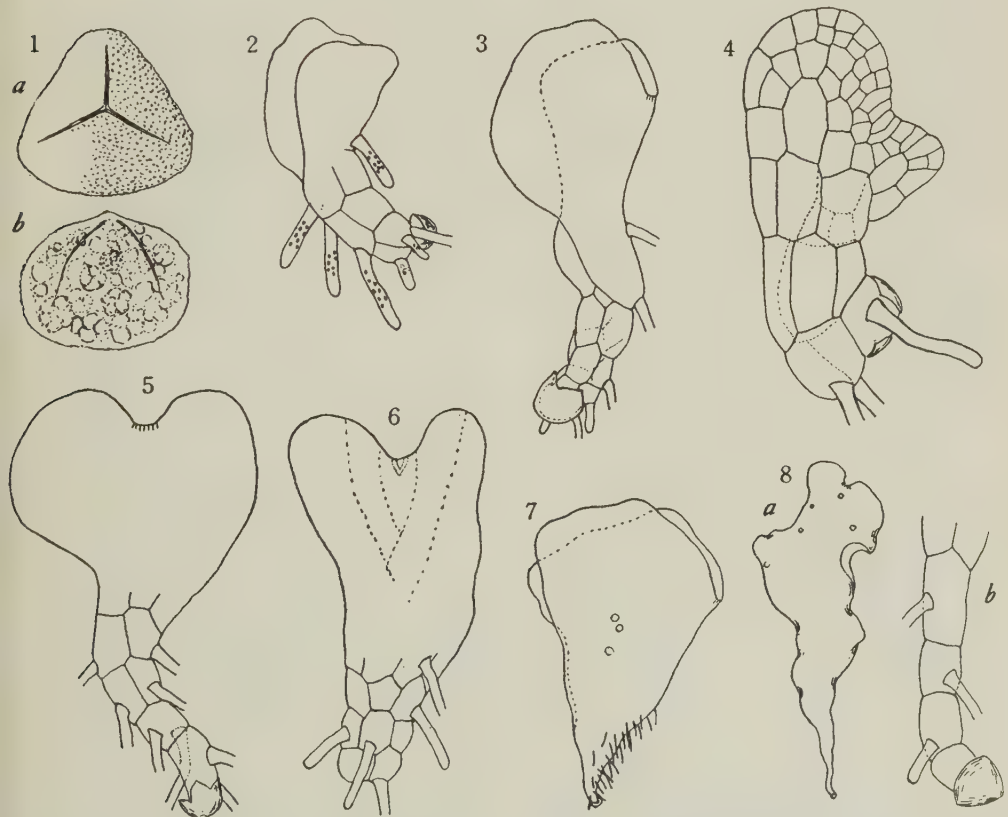
The genus *Matonia* R. Br., now looked upon as monotypic (Copeland, 1947), and the less known genus *Phanerosorus* Copel. constitute the family Matoniaceae R. Br. Although a considerable amount of attention has been given to the morphology and anatomy of the sporophyte of *Matonia pectinata* R. Br., the observations on the gametophyte have been limited to the statement "A green prothallus of the usual type has been seen attached to young sporelings" (Bower, 1926). The statement is accompanied by a figure of a young gametophyte bearing a sporeling, collected by Lang.

This investigation is based on cultures made from spores for which we are indebted to Professor R. E. Holttum who sent us from Singapore in January 1951 a fine collection made on Kedah Peak by Dr. Wolfe. The spores were planted immediately, some on distilled water, some on porous clay crock standing on peat, and some on peat. There was sparse germination on peat, very sparse on clay crock, and none at all on water. The meagre germination may have been caused by the delay between collecting and planting, but this does not seem to be a complete explanation, in view of the fact that spores planted one month later gave as good germination as the first planting. However, a third planting two months later was not as good, and no later plantings gave any germination. The germination was very slow but growth afterwards was not notably so. After the first few months the cultures were treated with Knop's solution as a supplementary source of mineral salts.

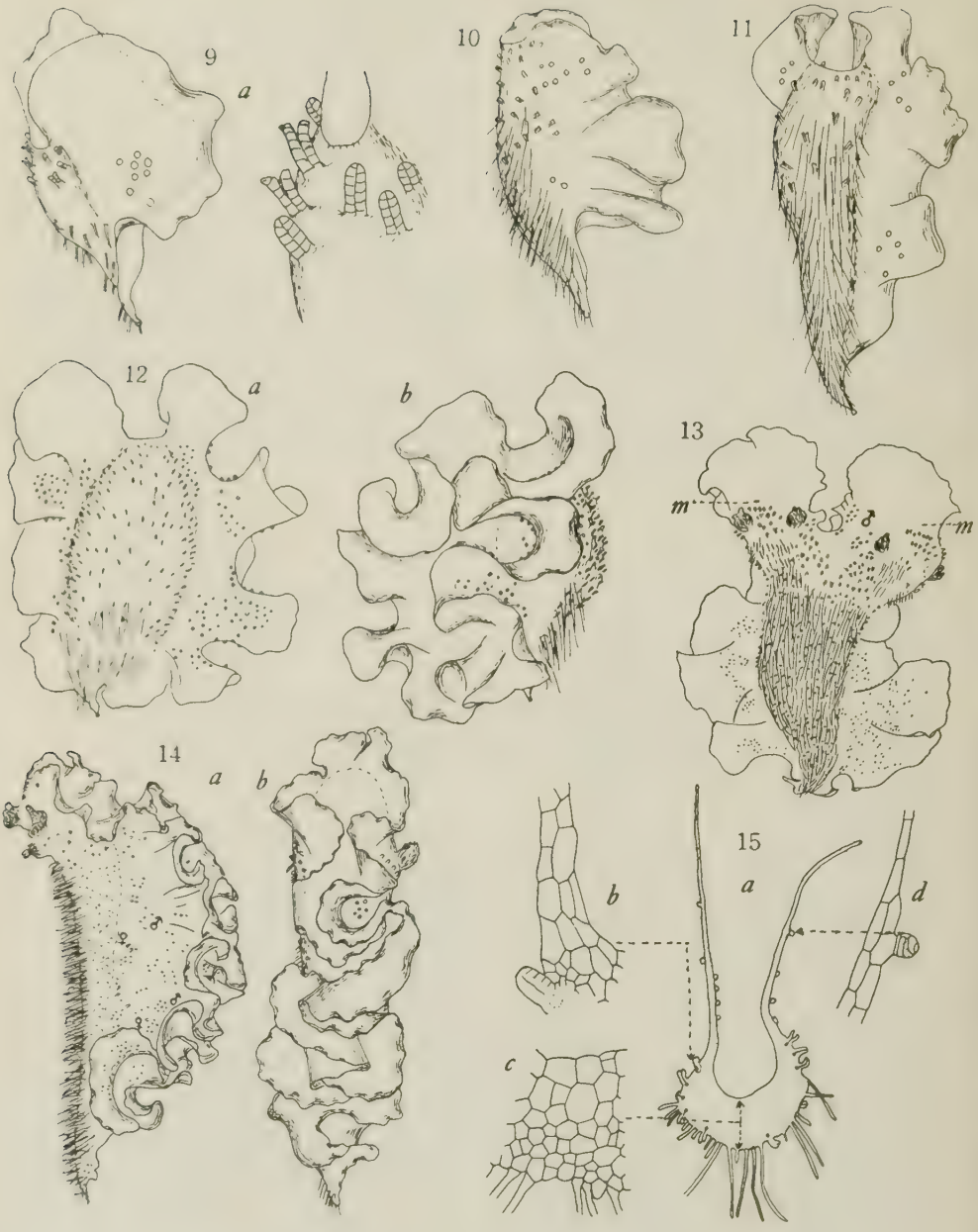
The techniques for the microscope preparations were the same as those described for *Stenochlaena palustris* (Stokey & Atkinson, 1952).

The spore of *M. pectinata* is of the tetrahedral type with a lightly roughened surface, a distinct tripartite ridge, and a diameter of 54-62 μ (Fig. 1*a*, *b*). The spores are colourless singly but appear pale yellow in mass; they contain granules which are often compound; oil drops are found when the spores are crushed. Although the collection of spores was abundant, it was soon evident from the appearance in water cultures that, as indicated by the form and contents, there was a large percentage of non-viable spores. No germination was obtained on water although for many weeks some of the spores had the appearance of being viable. Germination was not detected on peat or crock until about two months after planting. By that time the gametophytes had attained the stage shown in Figs. 2 and 3. Germination was so meagre in proportion to the number of spores planted, that we were reluctant to remove many gametophytes at this stage or to disturb the cultures hunting for younger stages. To judge from the stage in 9-10 weeks and the subsequent rate of growth, it seems probable that germination began 4-6 weeks after planting.

Without seeing the earliest stages it is possible from the form of the young gametophyte to make some inferences about the type of germination; the appearance of the base is a fairly safe guide. If there is a favourable amount of light and adequate space, it seems highly probable that on germination there is formed a mass (Figs. 3, 4), or a



FIGS. 1-8 — Fig. 1*a*, *b*, spore, two views. × 350. Figs. 2, 3, gametophytes 64 days after sowing spores. Fig. 4, 66 days. Fig. 5, 71 days. Fig. 6, 81 days. Fig. 7, 88 days; thallus with antheridia. × 18. Fig. 8*a*, 4 months; thallus with antheridia, from a clump; *b*, base of *a*.



FIGS. 9-15 — Mature gametophyte. Fig. 9*a*, 15 weeks after sowing spores; *b*, apical region of *a*, midrib with archegonia. Figs. 10, 11, 5 months. × 10. Fig. 12, 7 months; *a*, ventral view; *b*, dorsal view slightly tilted. Fig. 13, 12 months; two apical meristems, *m*; four young sporophytes. × 5. Fig. 14, 12 months; thallus with four sporophytes; *a*, lateral view; *b*, dorsal view. × 5. Fig. 15*a-d*, 12 months; *a*, c.s. thallus; *b*, wing, near midrib; *c*, midrib; *d*, wing halfway to margin.

plate (Fig. 6). If conditions are less favourable, there is a filament formed on germination (Figs. 5, 8). The thallus in Fig. 5 grew in a depression below the general level of the peat; that in Fig. 8 was in a clump. Subsequently there develops a plate one cell thick, even if the base is in the form of a mass. The thallus is flat for a very short period; the wings soon curve backward and then the plate forms a hinge-like thallus with a sharp fold (Figs. 2, 3 & 7). The fold makes it difficult to get a satisfactory view of the apical region, since the thallus does not flatten readily without splitting. In the young thallus there is undoubtedly an apical cell present for a certain period (Fig. 4), and although there were few gametophytes in which it could be seen, there were several which gave strong indications of the regular segmentation associated with the activity of a wedge-shaped apical cell (Fig. 6). The apical cell is later replaced by a marginal meristem (Figs. 5, 7 & 8).

The rhizoids on a young thallus, which are pale at first and contain many chloroplasts (Fig. 2), soon turn brown, usually a reddish or chestnut brown, and develop conspicuously heavy walls. The rhizoids are abundant and well developed even on early stages of the thallus (Figs. 2, 3, 5 & 7).

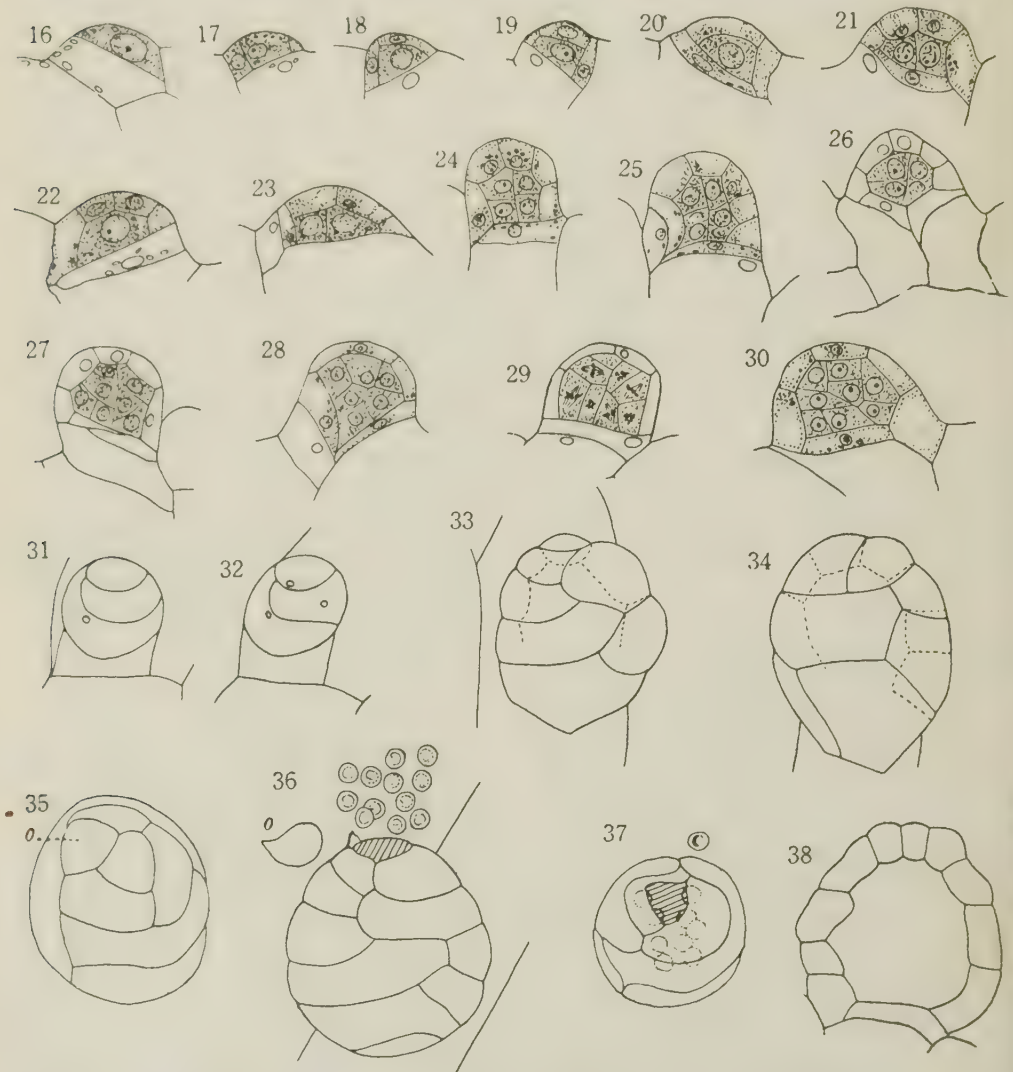
The curvature of the wings is not dependent on the midrib, since the thallus becomes hinge-like before the midrib is formed (Figs. 2, 3); but after the midrib is formed, the fold is more pronounced and is more difficult to flatten. The midrib is relatively broad even on young gametophytes which have borne only a few archegonia (Fig. 9). The wings are well developed and even at this stage the meristem is in a deep notch. The coarse stiff rhizoids are so abundant that they almost conceal the base. The midrib is not heavy at this stage. The wings develop vigorously with a margin which is slightly irregular or sinuate for some time (Fig. 9). With the continued growth of the gametophyte the wings enlarge so extensively both in breadth and length that they form coarse ruffles in large loose folds (Figs. 10-14). The wings are lifted high above the midrib (Fig. 15*a-d*), so that an old thallus growing on peat has a tendency to overbalance, and part of the cushion with its sex organs may be visible in combination with a view of the dorsal surface (Figs. 12*b*, 14*b*). The extensive thickening of the base of the wings probably assists in maintaining their more or less erect position (Fig. 15*a*, *b* & *d*). In this thallus, 12 months old, the midrib was 6-8 cells thick, but in older gametophytes it may be as many as 11 cells thick. In some cases the thickness of the midrib is not caused by a great increase in the number of cells; although there may be a large number of cells on the ventral side of the thallus, on the dorsal side there is a small number of relatively large cells. Some gametophytes, 12-15 months old, may be 13-16 mm. long; others may show dichotomous branching of the cushion. The gametophyte of *Matonia* has a strong resemblance to that of *Dipteris conjugata* (Stokey, 1945) and also to that of the Gleicheniaceae (Campbell, 1908, Stokey, 1950), although the wings are more coarsely ruffled and more markedly erect. Perhaps this is related to the fact that the wings become uplifted at a much earlier age in *Matonia*. The habit of *M. pectinata*, as it appeared in our cultures, is distinctive and not to be confused with that of any other known gametophyte. There were no hairs found on the gametophyte at any time.

Antheridium

The gametophyte is monoecious. The antheridia are of the primitive type of the leptosporangiate ferns — the large complex type already known in *Osmunda* (Campbell, 1892), *Dipteris* and the Gleicheniaceae. In *Matonia*, also, they show considerable variation in size. On the young thallus they are produced on the ventral surface of the wings (Figs. 9-11), but when the ruffling wings cover the midrib, the antheridia are also borne on the dorsal surface (Figs. 12*b*, 14*b* & 15*a*). In our cultures on peat, antheridia were produced continuously throughout the life of the gametophyte even after young sporophytes had appeared (Figs. 13, 80). This is unlike the higher ferns,

in which ameristic thalli among the older gametophytes usually provide the spermatozoids.

The development of the antheridium proceeds from an initial cell cut obliquely from a superficial cell of the thallus (Figs. 16-30). A series of walls in varying positions cuts off an outer layer of cells from the inner spermatogenous cell (Figs. 17-20, 22). In our material the basal cell is not one of the first cells cut off from the initial (Figs. 17-19, 23). External views of the young antheridium show that the curving of the wall cells occurs early in development (Figs. 31, 32); this increases as the antheridium grows (Figs. 33-36). The wall cells continue to divide (Fig. 40), and ultimately



Figs. 16-38 — Antheridium. Figs. 16-30, development of antheridium. Figs. 31, 32, external view of young antheridium. Figs. 33-35, external view of mature antheridium. Figs. 36, 37, dehiscence, lateral and top views; *o*, operculum. Fig. 38, median section of mature antheridium showing wall cells. All × 320.

there may be a large number of cells in the wall (Figs. 35-38). Eventually there is formed a small opercular cell which is thrown off when the antheridium opens (Figs. 35-37).

An examination of the developing spermatogenous cells reveals the essentials of the story of metamorphosis of the spermatid already reported in a few species of ferns by Allen (1911), Yuasa (1938), Rankin (1934) and others. Scarcity of material prevents us from throwing light on the unsolved and controversial problems concerning this process. In studying antheridial sections of *Matonia* one becomes aware of the fact that the nucleoli in the cells of certain partly grown antheridia are very prominent; the antheridium seems filled with large black dots. An examination under oil immersion invariably reveals two small but deeply staining granules in the cytoplasm on opposite sides of the nucleus (Figs. 39, 40). Although there is uniformity of development within each antheridium, the cutting must be fortunate to show both granules in the same plane. From the general aspect of the antheridium we judge these cells to be spermatid mother cells, although divisions were not observed to substantiate the statement. In the cytoplasm of the spermatid, that is the cell which will develop directly into the spermatozoid, we find one deeply staining granule, the blepharoplast (Figs. 41, 42); it increases in size (Fig. 41*a-c*) and elongates in the cytoplasm to follow the contour of the nucleus (Figs. 43, 44*a*). A cross-section of this structure (Figs. 44*b*, 46) shows it to be a broad band. As the nucleus of the spermatid begins to form a spiral (Figs. 45, 46), the

FIGS. 39-49 — Fig. 39, spermatid mother cell. Fig. 40, antheridium, spermatid mother cell stage. Fig. 41*a-c*, spermatid cell. Fig. 42, antheridium containing spermatids. Fig. 43, spermatid cell; elongation of blepharoplast. Fig. 44, spermatid cell; *a*, l.s. of blepharoplast; *b*, c.s. of blepharoplast. Fig. 45, spermatid cell, later stage. Fig. 46, spermatid cell, posterior coil of nucleus. Fig. 47, free-swimming spermatozoid. Fig. 48, mature spermatid; *a*, lateral view; *b*, seen from above. Fig. 49, l.s. mature antheridium. All × 1000 except Figs. 40, 42, 49.

chromatin condenses, and the nucleolus, although still visible, appears much smaller. The dark-staining band continues to grow along the nucleus and becomes the " border-brim " of Dracinschi (1930) in the mature spermatozoid (Figs. 47, 48). During this process the spermatid cells lose their angular shape (Figs. 44*a*, 46 & 49); they round up, the material between them staining with orange G and fast green. The cytoplasm of the cells also seems to contract (Figs. 45, 46), and in the mature spermatid the largest amounts of it appear, in our sections, only in the region more or less within the coils of the spermatozoid (Fig. 48).

The spermatozoid output is large, and, as seems to be the case in large antheridia, the total number is not discharged in one continuous stream. About a third of the spermatozoids are extruded within the spermatid envelopes. They lie in a mass for a short period, then are freed abruptly and swim rapidly away. After an interval, apparently used for rebuilding the necessary pressure, a second series of spermatozoids is extruded; these are freed from their envelopes immediately. The remaining fifty or so swim out of the antheridium, and the empty envelopes (" vescicles " of some authors) are extruded separately. Sometimes the last few spermatozoids are stuck inside the antheridium, twirl round and round, but are never released.

The free-swimming spermatozoid (Fig. 47) in stained material shows a relatively long nucleus which does not, however, reach the anterior end of the body and is bluntly pointed at the posterior end. The nucleus does not stain uniformly. The border-brim can be seen reaching from the anterior end of the spermatozoid to a point about two-thirds along the body where it merges with the nucleus. Numerous cilia arise from granules clearly arranged in a line between the nucleus and the border-brim.

Archegonium

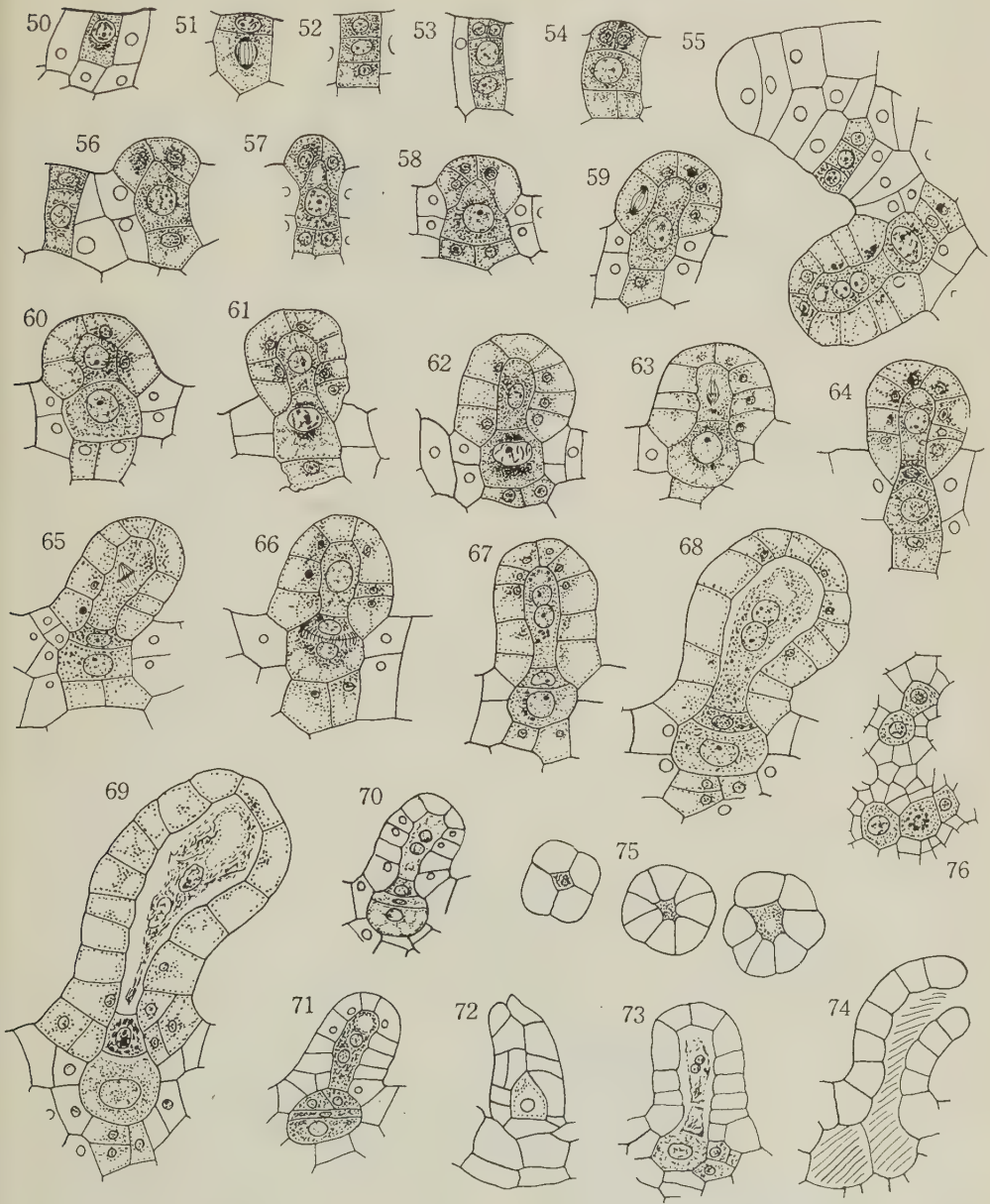
Archegonia are produced abundantly, and as many as 122 have been counted on one side of such a thallus as that shown in Fig. 14. The long necks are tilted toward the anterior end of the thallus (Fig. 9*b*) sometimes extending beyond the notch as in the Gleicheniaceae. They curve forward in an arc following the ventral bulge, and, consequently, median longitudinal sections are difficult to obtain.

The archegonium develops from an initial cell on the midrib very close to the apical meristem, and follows the usual pattern of development (Figs. 50-67). The division of the neck canal nucleus may take place either before or after the ventral canal cell is formed (Figs. 62-66), as has been described for other ferns (Stokey & Atkinson, 1952). The mature archegonium (Figs. 68, 69) is a massive structure although developed from a small initial (Fig. 50). The long neck often shows as many as nine cells in a tier; the tip is bulbous, as in the archegonia of higher ferns. There is a vacuole at the tip of the canal which increases in prominence as the tip enlarges (Figs. 67-69). Cross-sections show the anticlinal divisions which may take place in each of the four tiers thus accommodating the large neck canal within (Fig. 75). The lowest cells of the neck, the gametophyte cells adjacent to the egg, and the basal cells of the archegonium divide in such planes that they provide the egg with a complete jacket at maturity (Fig. 69). Archegonia may form close together without the typical layer of cells separating the eggs in the archegonia (Fig. 76). Such archegonia develop separate necks, and fertilization may occur as readily as in any other archegonia. The two sporophytes at the left in Fig. 14 may have arisen from such archegonia.

On old gametophytes anomalous structures appear, as is to be expected. The most frequent of these is the doubling of the ventral canal cell (Fig. 70); Fig. 71 may also be interpreted as a multiplication of the ventral canal cell. There may also be a change in the cytological aspect in one or more cells in the thallus adjacent to the egg (Fig. 73); the nuclei of these cells enlarge, the cytoplasm becomes dense, and they take on the aspect of the egg; this type does not mature (Fig. 74). It is doubtful if any of the anomalous

archegonia do. Such an anomalous archegonium as that in Fig. 72 may be found among the antheridia on the thickened base of the wings.

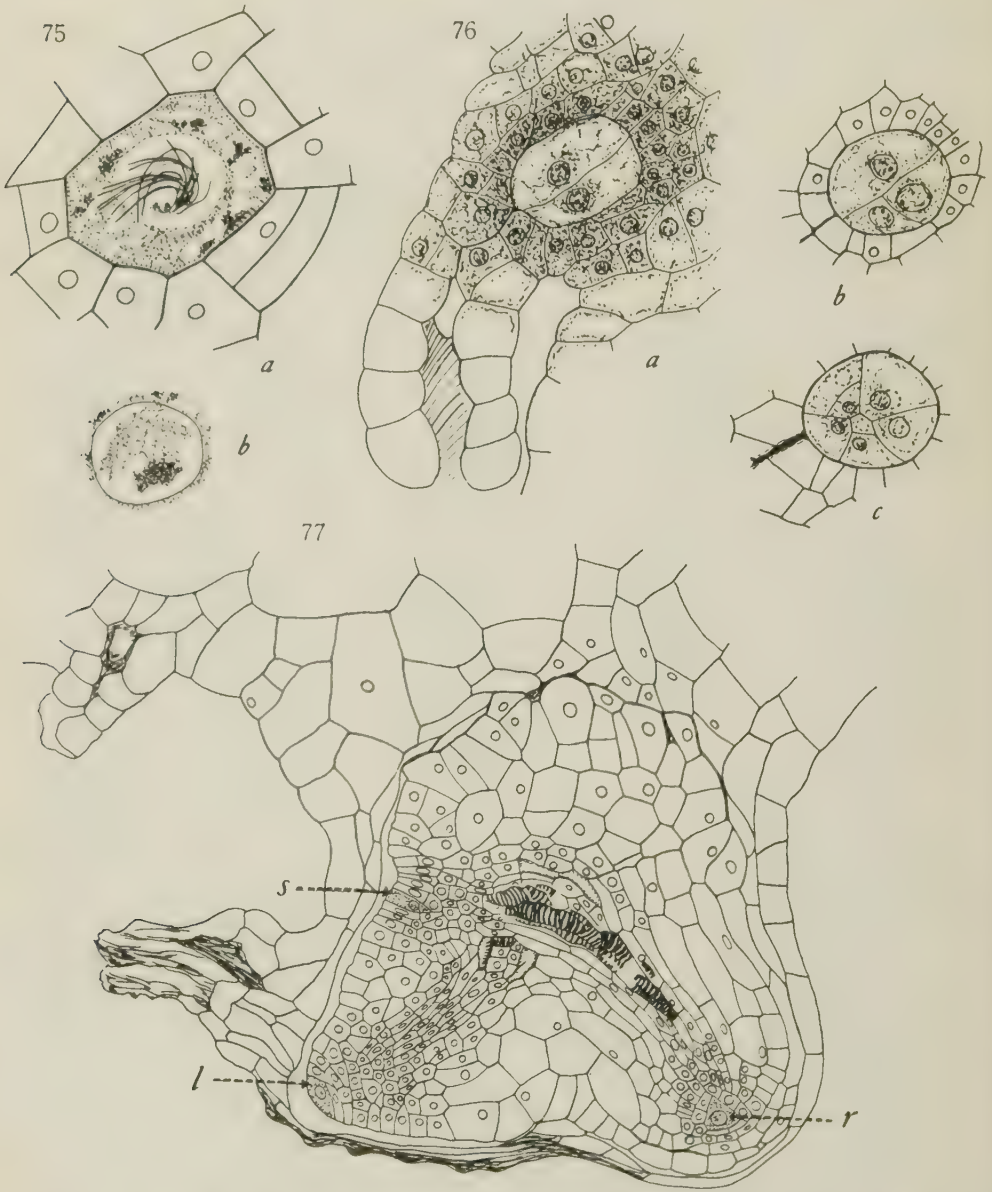
When conditions are favourable, the majority of the archegonia open, spermatozoids may enter and fertilization is effected. During the process the blepharo-



FIGS. 50-76 — Archegonium. Figs. 50-67, development of archegonium. Figs. 68, 69, mature archegonium. Figs. 70-74, anomalies. Fig. 75, c.s. neck of mature archegonium, before and after anticlinal divisions. Fig. 76, c.s. thallus showing egg cells. Figs. 50-69 × 320. Figs. 70-76 × 150.

plast and cilia are left in the cytoplasm (Fig. 75), as the junior author has found in *Lygodium* (Rogers, 1926) and in *Marsilia* (Atkinson, 1943).

Unfortunately the scarcity of material, especially in the early stages of the thallus, has ruled out chromosome counts. The nuclei are small, but fortunate polar



FIGS. 75-77 — Fertilization and embryo. Fig. 75, c.s. of outer region of egg; *a*, high focus showing blepharoplast and cilia in cytoplasm; *b*, low focus showing nuclei within the nuclear membrane of egg. × 700. Fig. 76*a-c*, young embryos. × 320. Fig. 77, embryo shortly before rupture of archegonium; *s*, apical cell of stem; *r*, apical cell of first root; *l*, one of the initials of first leaf.

views of metaphase plates in one antheridium and one young archegonium make it possible to say that the gametophytic count is about 26. Many of the chromosomes appear to have terminal or subterminal attachments.

Embryo

The first division of the fertilized egg is in the plane of the neck of the archegonium, and perpendicular to the longitudinal axis of the thallus (Fig. 76). It divides the cell into two nearly equal parts. This agrees with the observations of Vladesco (1934) and others for leptosporangiate ferns. There was not material for a detailed study of the divisions which follow. A mass of cells is formed within the venter of the archegonium (Figs. 77, 78); in this mass appear the apical cells of the stem and root, and the group of initials of the leaf one of which is visible in Fig. 77. Vascular tissue is differentiated at the centre of this mass of cells. A reconstruction (Fig. 78) of the embryo sectioned for Fig. 77 shows that the xylem forms a solid core at the centre of the embryo. In view of the complex solenostelic anatomy of the adult sporophyte it is interesting to find xylem elements well differentiated before the embryo is large enough to have broken through the venter (Figs. 77, 78). A cursory examination of the literature indicates that this is a precocious development of xylem tissue (Vladesco, 1934; Campbell, 1940). The embryo grows and ruptures the venter. Branches from this central mass of vascular tissue lead to the second and third leaves, and to roots as they develop.

It has been mentioned above that gametophytes, 12 months old, are vigorous and still bearing functional eggs and spermatozoids, and that fertilization can take place whenever water is supplied. Several thalli such as these were put in a watch glass for observation and watered from time to time. At the end of a month each thallus had produced as many as four embryos (Fig. 79), and these were similar to those left undisturbed on peat and flooded once at the beginning of the experiment. In the latter case all the embryos are of approximately the same age (Figs. 13, 14*a*), but those submitted to successive waterings showed embryos of different ages (Figs. 79, 80).

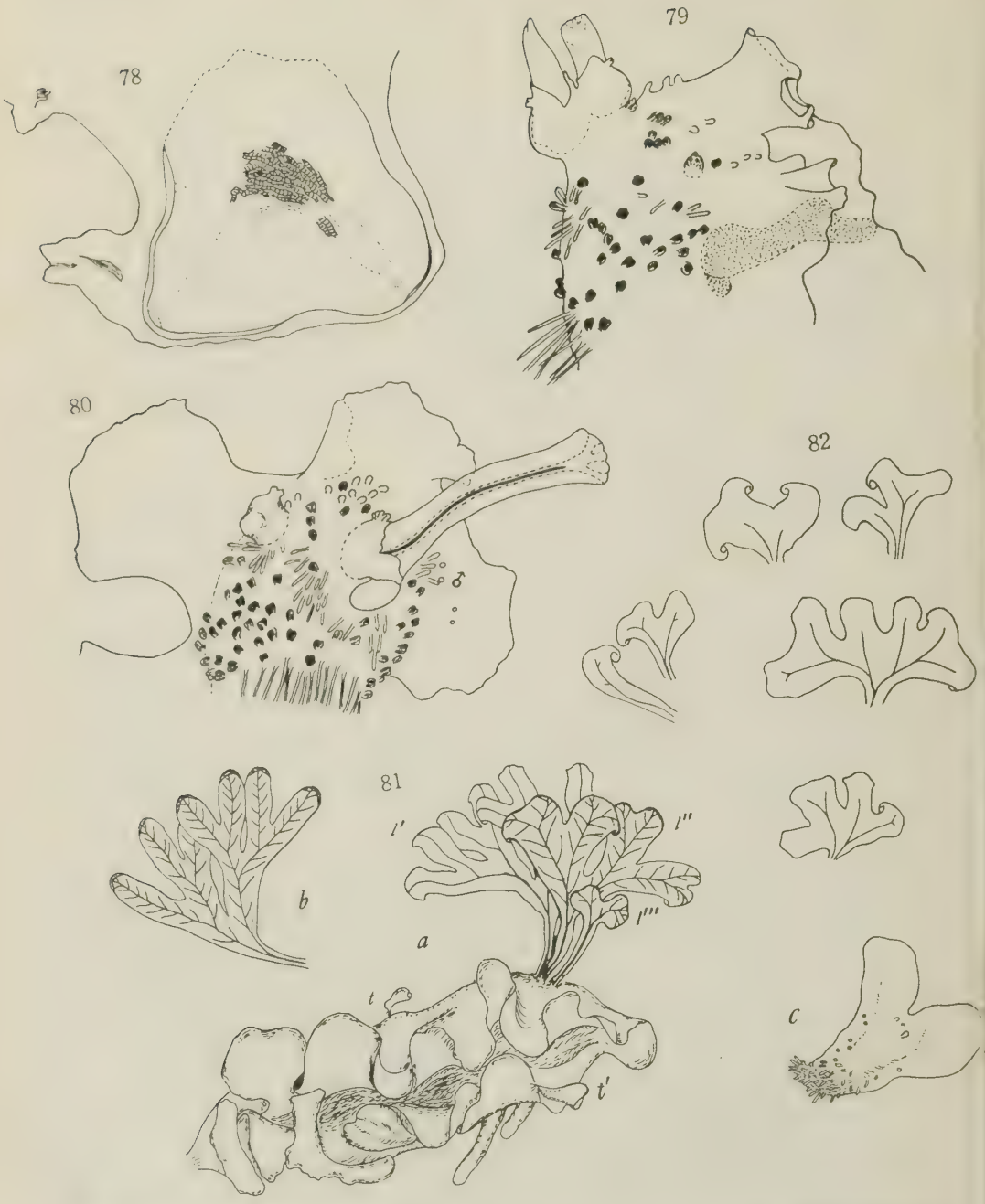
The young sporophytes in our cultures grew slowly, and the oldest of them, now 6 months old, has only three leaves (Fig. 81). The first leaves show variation in lobing (Fig. 82); the venation is dichotomous at first.

Gametophytes, 15 months old, show regenerated thalli produced both from the cushion and from the margins at the posterior end. These regenerated thalli (Fig. 81*t*, *t'*) are present even on gametophytes which are bearing sporophytes. They are like those grown from spores — the wings are strongly recurved, they bear reddish brown rhizoids, and both kinds of sex organs.

Discussion

Accounts of *Matonia* and discussions of its systematic position rarely fail to point out the similarities to *Gleichenia* and *Dipteris*. These comparisons, based on the sporophyte, are just as inevitable when the development and structure of the gametophyte is considered. There may be a mass, plate or filament on germination, with the filamentous type the least common. This range in type of germination allies *Matonia* to the primitive ferns rather than to the higher ferns.

In the mature gametophyte the ruffled uplifted wings of *Matonia* suggest the gametophyte of the Gleicheniaceae, known in four genera (Campbell, 1908; Stokey, 1950) and of *Dipteris conjugata* (Stokey, 1945). The ruffling of *Matonia* is of a coarser type and is sufficiently distinct in aspect to identify it in most cases. This type may be related to the fact that the wings become uplifted at a much earlier stage in *Matonia*, and the base of the wing is more heavily thickened. The heavy midrib is found in all three groups; this is characteristic of primitive ferns. Although there is a considerable range in the thickness of the midrib in the higher ferns (the Polypodiaceae, *sensu lato*), the thin type is apparently of most common occurrence, and the midrib



FIGS. 78-82 — Fig. 78, diagram of section of embryo showing central core of vascular elements (reconstruction). × 40. Figs. 79, 80, anterior end of gametophyte with young sporophytes. × 10. Fig. 81*a-c*; *a*, gametophyte with regenerated thalli, *t*, *t'*; and sporophyte with first three leaves, 1', 1'', 1'''; *c*, regenerated thallus, *t'*, spread out. Fig. 82, young leaves showing variation in lobing.

rarely attains a thickness found in the primitive ferns. In all the three families mentioned — Matoniaceae, Gleicheniaceae and Dipteridaceae — the rhizoids are abundantly developed on the midrib of the mature thallus and are of heavy texture, reddish brown or chestnut brown in colour.

The gametophyte of *Matonia* is like that of *Dipteris* in being naked throughout its life, while that of the Gleicheniaceae, so far as is known, possesses a specialized and distinctive type of hair at some stage in the development of the gametophyte.

The sex organs of *Matonia* show a strong resemblance to those of *Dipteris* and the Gleicheniaceae. In all of them the antheridia are large with a large spermatozoid content, and a wall consisting of many cells. The mature archegonium is of the same type in all the three families. The development agrees in general with that of the leptosporangiate ferns, but the mature archegonium has a long neck which is inclined forward. This type has not been described for any fern except *Matonia*, *Dipteris* and the Gleicheniaceae, and it is decidedly unlike the straight neck of the Osmundaceae (Campbell, 1892), or that of the higher ferns, in which the neck is shorter and is inclined toward the base of the thallus. The bulbous form of the tip of the neck, which is related to the anticlinal divisions in the cells of the neck, is more marked in *Matonia* than in *Dipteris* or the Gleicheniaceae; in that respect *Matonia* has greater similarity to the higher ferns.

The extent to which polyembryony is developed is suggestive of the lower ferns. In many ferns, especially the higher ferns, on the development of a young sporophyte apical meristematic growth ceases (Allen, 1911; Albaum, 1938), and consequently no more archegonia are formed. *Matonia* is closer to *Osmunda* in this respect. Goebel (1930) mentions that old band-shaped gametophytes of *Osmunda* may show polyembryony. We have had examples of this in our own cultures of the Osmundaceae, the account of which will appear later. Rauwenhoff (1898) reported polyembryony in the Gleicheniaceae. Cases of polyembryony have been noted in a few species of higher ferns, such as those obtained by Mottier (1925) in experimental cultures of *Dryopteris mollis* (Jacq.) Hieron. and *Matteuccia nodulosa* (Michx.) Fernald, as well as in *Osmunda claytoniana* in which the gametophytes developed to an unusual size. Many of the sporophytes, however, were on cordate marginal outgrowths from the midrib and not on the original midrib. The ability to produce several sporophytes on the original midrib is apparently a function of massive gametophytes, such as are most common in the more primitive ferns.

The characteristics of the gametophyte of *Matonia* are sufficiently like those of *Dipteris*, as exemplified by *D. conjugata* Reinw., to indicate that the Dipteridaceae (Seward & Dale, 1901) has a much closer affinity to the primitive families Matoniaceae and Gleicheniaceae than to such higher families as the Polypodiaceae *sensu stricto* (Copeland, 1947). In *Matonia* the continued and abundant production of sex organs, the ability of the large and long-lived thallus to support more than one sporophyte, and the presence of a young sporophyte with well-developed leaf and root side by side with maturing and functioning sex organs, point downward to the primitive groups rather than upward toward the higher ferns.

Summary

The gametophyte of *Matonia pectinata* was studied in cultures raised from spores, which germinated slowly giving rise to a mass, a plate or a filament. This was followed by a cordate thallus in which there was early and persistent recurving of the large wings. Gametophytes, 6-15 months old, had coarsely ruffled wings, a thick broad midrib, a heavy growth of reddish brown rhizoids, and occasionally a forking tip. No hairs were present at any stage. Antheridia are abundant even on old thalli; they are of a large primitive type with a many-celled wall, and a large sperm output. Archegonia are also produced abundantly; they have long necks inclined forward. Fertilization occurred readily, and polyembryony was common

on old gametophytes. The first division of the fertilized egg is in the plane of the neck of the archegonium and perpendicular to the longitudinal axis of the thallus. Vascular tissue appears in the embryo before it has broken through the venter. In type of germination, form of mature thallus, size and structure of antheridium and archegonium, the gametophyte of *Matonia* has much in common with that of the Gleicheniaceae and the Dipteridaceae. The gametophytic chromosome number is about 26.

Part of the work of the senior author was carried on at the Marine Biological Laboratory, Woods Hole, Mass.

The junior author wishes to thank the Biology Department of Amherst College for many courtesies and certain technical assistance.

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FLORAL MORPHOLOGY AND EMBRYOLOGY OF *PSILOSTACHYS SERICEA* HOOK. F.

T. S. BAKSHI
Birla College, Pilani, India

Introduction

The genus *Psilostachys* (Amarantaceae) comprises three species of which one, *P. sericea,* occurs in India (Hooker, 1885).

Schnarf (1931) has reviewed the earlier embryological literature on the Amarantaceae. He includes the works of Hofmeister (1859), Braun (1859), Fischer (1880), Guignard (1882) and Dahlgren (1916). Woodcock (1931) studied the seed development of *Amarantus caudatus.* Naithani (1933) and Joshi and Rao (1934) investigated the embryology of *Digera arvensis* which was reinvestigated by Puri and Singh (1935) who corrected several previous mistakes. The development of the embryo of *Digera arvensis* and *Alternanthera sessilis* was worked out by Joshi and Kajale (1937). Kajale also gave a comparative account of the embryology of *Alternanthera sessilis* (1935), *Achyranthes aspera* (1937), *Celosia argentea, Allmania nodiflora, Amarantus viridis, Cyathula tomentosa, Pupalia lappacea* and *Aerua lanata* (1940b). Development of the embryo of *Amarantus caudatus* and *A. retroflexus* is known through the works of Souèges (1937a, b). Recently, Dambroise (1947) has given a detailed account of the endosperm development in many members of the Centrospermales including *Amarantus retroflexus* and *Celosia cristata.*

At the request of Prof. P. Maheshwari, Mr. B. S. M. Dutt of Kakinada (South India) was good enough to fix some material of *Psilostachys sericea* in December, 1950, in formalin-acetic-alcohol. This was kindly passed on to me for investigation. The outer perianth leaves and the testa of the mature seeds were removed to allow proper infiltration. Sections were cut 8-10 μ thick and stained in safranin and fast green as well as in iron-alum-haematoxylin. The former gave better results. Smear preparations of pollen were also studied.

Floral Morphology

Three to five bracts appear on the inflorescence axis in close succession and the floral primordia arise in their axils only after they have attained a considerable size. Bracteoles, perianth, stamens and carpels arise in acropetal succession. The tip of the floral axis differentiates into the single ovule. From its basal portion grows the ovary wall which encloses the ovule and extends into the hollow style.

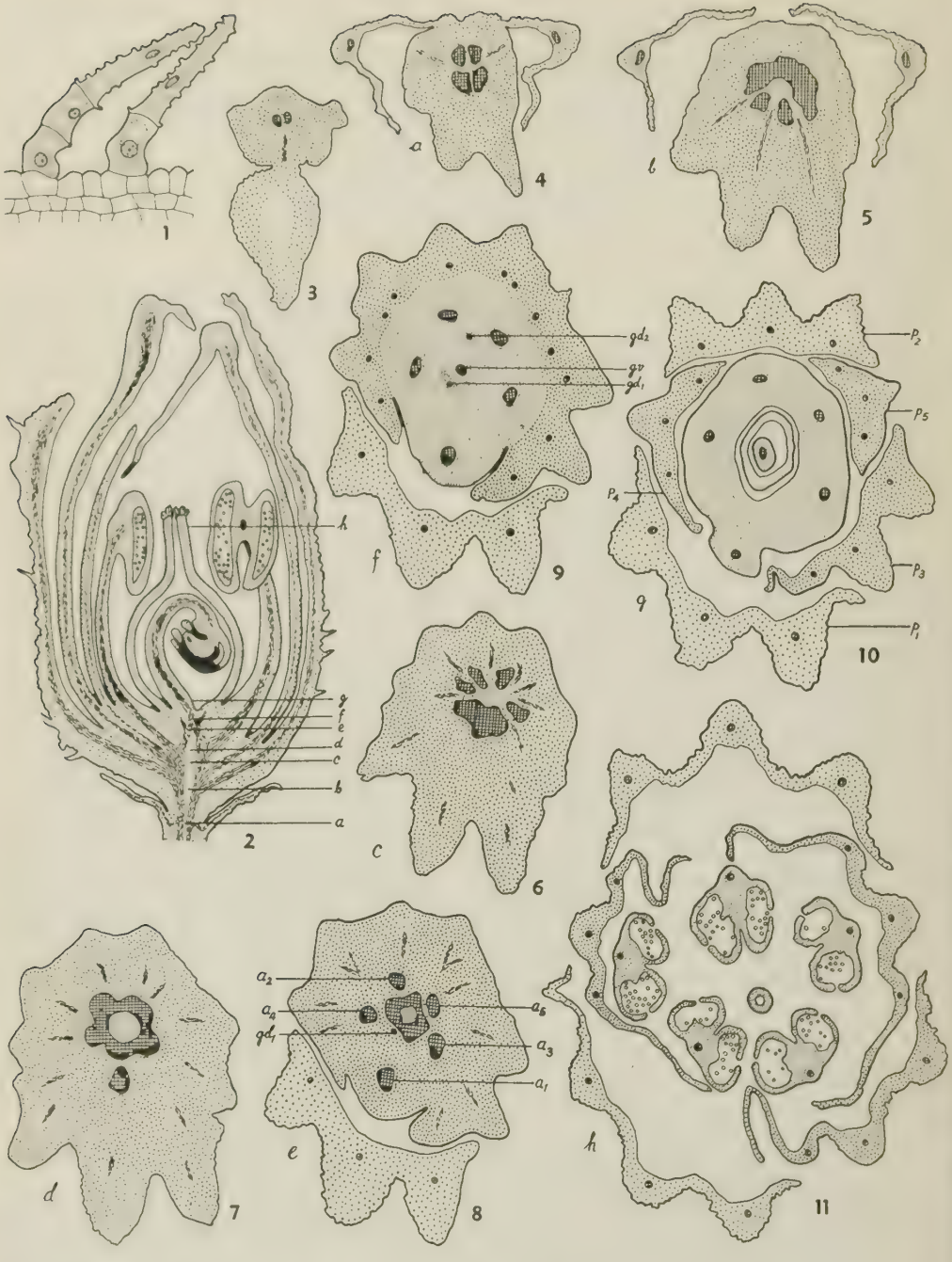
Six to eight minute, subsessile flowers are arranged on a short, slender and zigzag rachis. Each is subtended by a bract and two small bracteoles. The perianth comprises five segments of which the outer two are the largest and show three prominent ribs. The outer epidermis bears numerous long, uniseriate, 2-7-celled hairs with characteristic warty thickenings on the terminal cell (Fig. 1).

The filaments of the five stamens are fused at the bases but free above. The anthers are four-celled. The ovary is ovoid and a little compressed. The hollow style has a slightly bilobed stigma with prominent papillae.

Vascular Anatomy of the Flower

In the pedicel the vascular supply to the bract runs parallel to the stele for a short distance before entering the bract (Fig. 3).

The pedicel shows two vascular bundles facing each other, as is also the case in the branch trace of most of the Amarantaceae (see literature quoted in Joshi, 1931).



FIGS. 1-11 — Morphology of the flower. p_1-p_5=perianth leaves, a_1-a_5=staminal traces, gd_1-gd_2=dorsal traces to the gynaecium and gv=ventral trace to the ovule. Fig. 1, epidermal hair from the outer perianth leaf. × 300. Fig. 2, l.s. flower. × 33. Fig. 3, t.s. pedicel showing bract-trace. × 33. Figs. 4-11, t.s. flower at levels *a*-*h*. × 33. Figs. 2-11 diagrammatic.

The two bracteole traces originate at a level somewhat higher than their bases and then descend to enter their respective organs (Figs. 2, 4). Unlike *Digera arvensis*, there are no scales in the axils of the bracteoles nor is there any trace of their vascular stubs.

The perianth traces arise in spiral succession (Figs. 5-10, p_1-p_5). Each perianth segment receives three traces, one median and two laterals. The lateral traces of adjacent perianth leaves usually arise conjointly.

After the departure of the perianth traces the stelar bundles again form a continuous ring. Each stamen receives a single trace which remains undivided[1]. The staminal traces arise in a spiral manner (Figs. 7, 8, a_1-a_5) so that the trace of the first stamen, a_1, is situated opposite to the perianth leaf p_1, that of the second, a_2, opposite to p_2 and so on. Hooker (1885) describes the stamens of *Psilostachys sericea* as free but actually they are fused at their bases to form a short staminal tube (Fig. 10).

After supplying the stamens, two traces arise from the stelar ring, one after the other, which reach up to the base of the ovary wall and are designated as the dorsal traces (Figs. 2; 8, 9, gd_1, gd_2). The rest of the stelar tissue unites to form the ventral trace, *gv*, which supplies the single ovule (Figs. 9, 10). Of the two dorsals, the first to originate, gd_1, is situated opposite to the perianth leaf p_1 and the second, gd_2, opposite to p_2. The former fades before entering the ovary wall while the latter is continued slightly further up but does not enter it (Figs. 2, 10, 11). The two dorsal traces and the single ventral trace lie, as in *Digera arvensis* (Joshi & Rao, 1934), almost in a straight line (Fig. 9). Joshi and Rao do not mention whether the two dorsals in *D. arvensis* originate at the same level or not, though their Fig. 9 (p. 206) suggests the former condition. In *Psilostachys sericea*, however, the two dorsals arise at different levels. It may, therefore, be presumed that the gynaecium in this plant is bicarpellary and that the two carpels are arranged spirally.

1. In *Digera arvensis* (Joshi & Rao, 1934) each staminal trace bifurcates in the region of the staminal tube, the branches uniting again as the filaments separate.

Microsporogenesis

The young anther lobe shows a hypodermal archesporium, 2-4 cells across in transverse section and 3-5 cells in longitudinal section, a condition similar to that reported in most other members of this family. However, in *Digera arvensis* (Puri & Singh, 1935) and *Pupalia lappacea* (Kajale, 1940b) there is only a single vertical row.

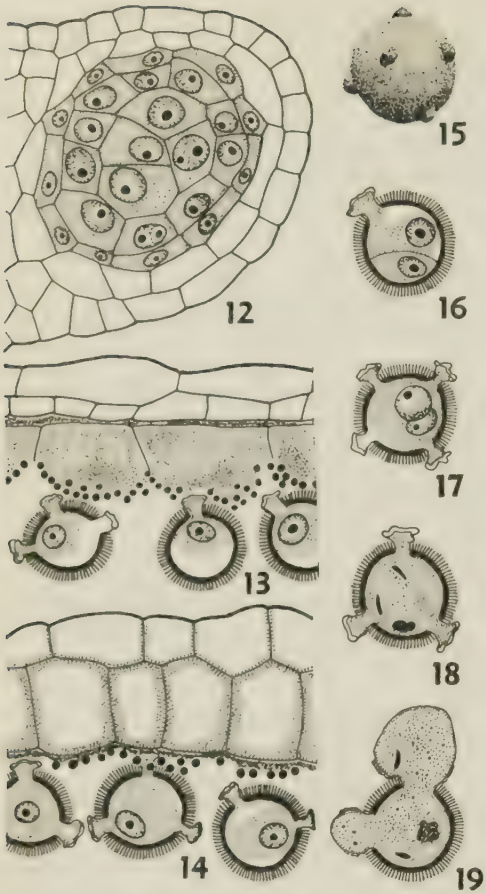
The archesporial cells enlarge and become richly protoplasmic. They divide periclinally to form the outer parietal and the inner sporogenous layers. The parietal layer divides again giving rise to the endothecium and an inner layer which divides once more to produce the single middle layer and the tapetum (Fig. 12).

The middle layer is the first to degenerate and by the time the pollen grains are uninucleate, it is already crushed (Fig. 13).

The tapetum is glandular and at the time of meiotic divisions in the microspore mother cells, the nuclei of the tapetal cells also divide mitotically so that they become binucleate. Occasionally tetranucleate cells may also be observed. Some of the nuclei were lobed and contained more than one nucleolus indicating that the nuclei may often fuse. In *Celosia argentea* (Kajale, 1940b) and *Digera arvensis* (Puri & Singh, 1935) the tapetal cells show as many as five nuclei.

The endothecial cells elongate radially and their walls become greatly thickened at the same time as the microspores are being formed. The characteristic fibrous thickenings are noticeable only at maturity when the pollen grains are about to be shed.

As the tapetum is gradually used up, minute, rounded, oily globules appear on its inner side and become conspicuous during the maturation of the pollen grains (Fig. 13). Finally as the tapetum becomes used up these globules come to lie on the inner wall of the endothecium (Fig. 14). The globules which stain brownish-yellow with haematoxylin and



FIGS. 12-19 — Microsporogenesis and development of male gametophyte. Fig. 12, t.s. anther lobe showing endothecium, middle layer, tapetum and microspore mother cells. × 1000. Fig. 13, l.s. part of anther lobe showing degenerated middle layer and tapetum with globular bodies. × 1000. Fig. 14, anther wall with enlarged endothecium, note position of globules. × 1000. Fig. 15, surface view of pollen grain. × 1200. Fig. 16, two-celled pollen grain. × 1200. Fig. 17, same with the intervening wall dissolved. × 1200. Fig. 18, three-celled pollen grain. × 1200. Fig. 19, germinating pollen grain from stigma. × 1200.

red with safranin, have also been reported in other plants of the Amarantaceae[2] and are of more widespread occurrence in angiosperms than was believed hitherto (see literature quoted in Maheshwari, 1950). Their exact nature and function is not understood but to a certain extent they might help in the formation of the exine.

The primary sporogenous cells divide once, sometimes twice, to give rise to microspore mother cells. As they prepare for meiosis their protoplasts recede from the mother walls which remain in contact with each other. A special mucilaginous wall appears between the protoplast and the original wall. Reduction divisions are simultaneous and cytokinesis takes place by furrowing (cf. Puri & Singh, 1935; Kajale, 1940b). The microspore tetrads are of three types — tetrahedral, isobilateral and decussate.

The special mucilaginous wall persists till microspore formation but is finally consumed liberating the microspores. The nature of this wall has attracted considerable attention. In *Psilostachys sericea* it appears to arise by the gradual swelling and gelatinization of the secondary layers of the original wall as well as by the secretion of the protoplast (cf. Farr, 1916; Castetter, 1925).

Male Gametophyte

The uninucleate pollen grain is full of cytoplasm and its wall consists of a thick smooth exine and a thin intine (Fig. 14). In the mature pollen grain the exine itself shows two layers, the inner of which is more darkly stained than the outer. There are six large and circular germ pores more or less equidistant from each other. The intine protrudes out appreciably through the germ pores (Figs. 15-18). In the Amarantaceae, psilate pollen grains with cribellate germ pores have also been recorded in *Celosia argentea, Allmania nodiflora, Pupalia lappacea* and *Aerua lanata* (Kajale, 1940b).

As the pollen grain enlarges, a large vacuole appears in the cytoplasm which pushes the nucleus to one side. It divides to produce a smaller generative and a larger tube cell separated by an ephemeral membrane (Fig. 16). After the dissolution of the separating wall, the lenticular generative cell moves up close to the tube nucleus (Fig. 17). The

2. Kajale (1940b), while remarking that none of the previous authors recorded them in *Digera arvensis*, has obviously overlooked Fig. 4 of Puri and Singh (1935).

mature pollen grain is three-celled (Fig. 18). The two male cells are spindle shaped. The tube nucleus assumes an irregularly lobed appearance and stains more or less homogeneously.

Ovule

There is a single crassinucellate, bitegmic ovule in each ovary. In the beginning the ovule is orthotropous but it soon curves until at the megaspore mother cell stage it becomes anatropous (Figs. 20, 21). The curvature, however, continues until the ovule has turned another 180° so that finally the micropyle faces the style (Figs. 22, 23) and the ovule becomes circinotropous[3]. The only other member of the Amarantaceae with similar ovule is *Deeringia celosioides* (Bhargava, unpublished MS[4]). After fertilization the embryo sac continues to enlarge and curve so that finally it becomes horseshoe shaped. From this point of view the ovule may be described as amphitropous.

Of the two integuments, the inner appears first and forms the micropyle. Both are two layered but the inner becomes more massive at the micropylar end. In *Celosia argentea, Amarantus viridis, Aerua lanata, Allmania nodiflora, Cyathula tomentosa* and *Pupalia lappacea* the outer integument is also several layered at the micropylar end (Kajale, 1940b). Both the integuments are separated by a wide air space at the chalazal end as is also the case in several other genera (cf. Kajale, 1937, 1940b). Occasionally, a second air space between the inner integument and the nucellus occurs in *Psilostachys sericea*, similar to that known in *Pupalia lappacea* (Kajale, 1940b).

Megasporogenesis

While the microspore mother cells are still in the resting condition, a hypodermal archesporial cell, or sometimes two such cells, differentiate in the young nucellus. Occasionally, one or two adjacent cells of the nucellus may also simulate the appearance of archesporial cells (Fig. 24). As a rule only one of them enlarges and divides periclinally to form the outer parietal and the inner megaspore mother cell (Fig. 25). Side by side, one or two cells of the nucellar epidermis may also divide periclinally. During the reduction divisions of the megaspore mother cell, the primary parietal cell divides, first anticlinally and then periclinally. Subsequent divisions may also occur but no conspicuous parietal tissue is formed.

The megaspore mother cell enlarges considerably and divides resulting in two dyad cells which divide once again to give rise to a linear row of four megaspores (Fig. 26). The chalazal functions while the remaining three degenerate. In two tetrads, the two central megaspores were of smaller size and were placed transversely (Fig. 27).

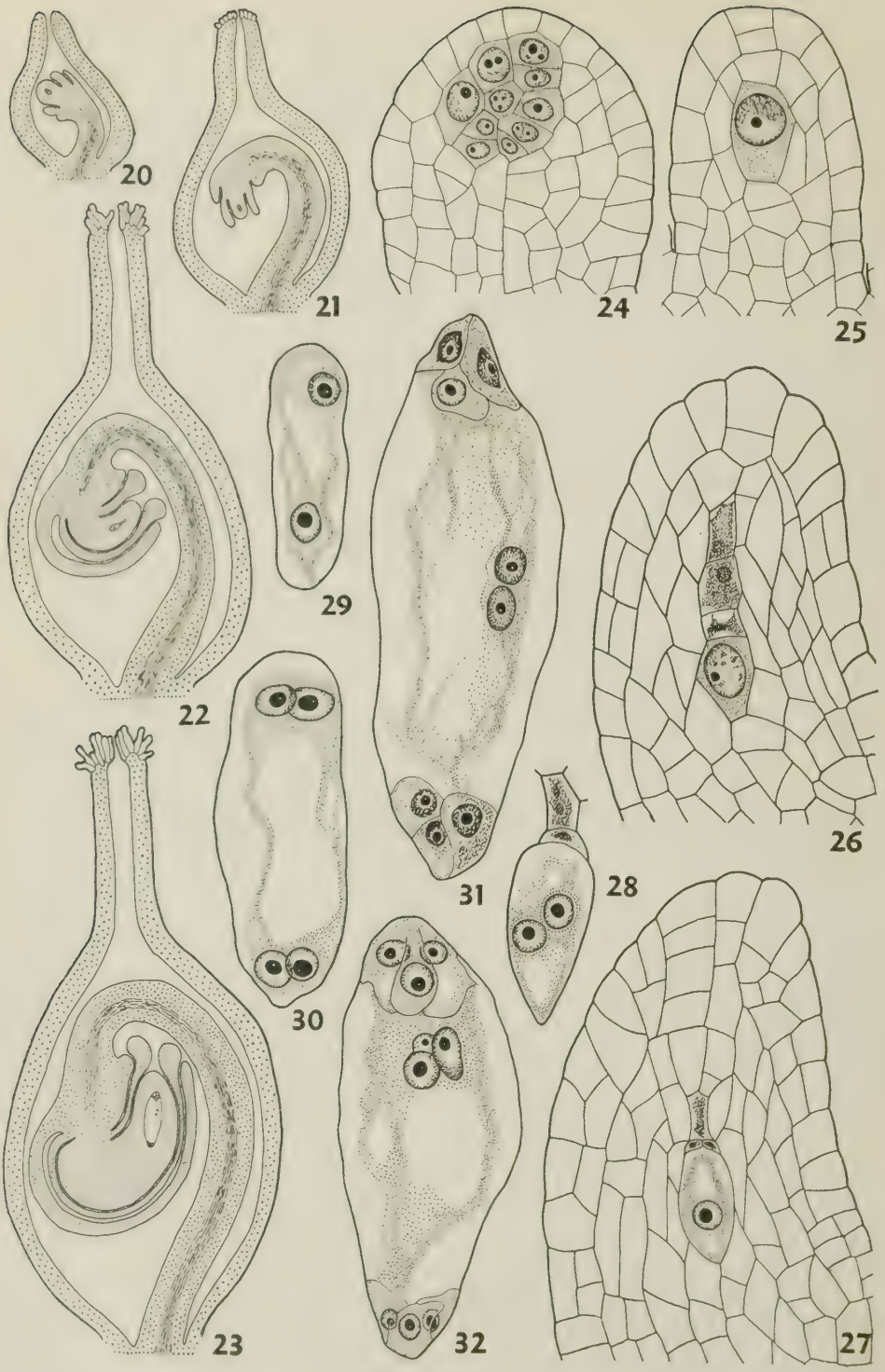
Female Gametophyte

The functioning megaspore elongates and becomes vacuolated and its nucleus comes to lie more or less in the centre (Fig. 27). It soon divides to give rise to the two-nucleate embryo sac (Figs. 28, 29). Subsequent divisions lead to the four- and eight-nucleate stages (Figs. 30, 31). The egg is flask shaped and protrudes below the hooked synergids whose nuclei are usually centrally placed with a large vacuole at the lower end. The three antipodal cells are ephemeral and disappear while the chalazal end of the embryo sac elongates to form a caecum (Fig. 33). The two polar nuclei fuse in the upper part of the embryo sac but the fusion nucleus may often shift its position. The embryo sac at this stage is straight, curvature taking place in post-fertilization stages.

The development of the embryo sac is of the 'Polygonum' type, as in other members of the family. An abnormal embryo sac showed the usual egg apparatus and antipodal cells but three, instead of two, polar nuclei were fusing near the egg (Fig. 32). The origin of the ninth nucleus could not be traced.

3. The ovule of *Opuntia aurantiaca* (Archibald, 1939; Maheshwari, 1950), which has been described as circinotropous, is really a step further in that here the curvature is of approximately 540°.

4. I am grateful to Mr. H. R. Bhargava for permitting me the use of his unpublished MS.



FIGS. 20-32

Pollination and Fertilization

According to Knuth (1909), who studied *Amarantus blitum*, pollination in the family Amarantaceae is anemophilos. On the other hand, Kajale (1940b) considers self-pollination to be more likely. In *Psilostachys sericea* also, self-pollination appears to be common. It was observed that though microsporogenesis starts much earlier than megasporogenesis, the three-celled pollen grains are not shed until the egg is ready to be fertilized and the glandular hairs of the stigma have reached their maximum activity. Several flowers with exembryonate seeds showed degenerated pollen grains in their anthers.

After deposition on the stigma, the intine of the pollen grain protrudes out through one of the germ pores to form a large globular vesicle into which the male cells move out first (Fig. 19). The vesicle elongates and gradually forms the tube. After the male cells have entered the tube, the tube nucleus also emerges from the pollen grain. Many pollen grains germinate on the stigma so that the hollow style is often crowded with pollen tubes. The tube nucleus could not be identified in pollen tubes traversing the stylar canal and in certain cases it could not be seen even in pollen grains germinating on the stigma. Probably the tube nucleus frequently degenerates even before pollination as is also indicated by its lobed structureless appearance. Kajale's (1940b) view that the tube nucleus takes part in the growth of the pollen tube is, therefore, untenable.

On reaching the ovary, the pollen tube passes through the micropyle, penetrates the nucellus and enters the embryo sac disorganizing both the synergids. It usually persists till the formation of a six-celled proembryo. In one ovule three pollen tubes were seen in the micropyle and two of these had entered the embryo sac. Accessory pollen tubes in the embryo sac have also been reported in several other members of the family.

Perisperm, Endosperm and Embryo

As the embryo sac elongates like a horse-shoe, it encloses the central part of the nucellus which persists in the mature seed as perisperm (Figs. 33-36). Its cells are full of starch and it forms the main storage tissue of the seed. A similar condition is known in other members of the family.

The primary endosperm nucleus divides prior to the division of the oospore and when the proembryo is six-celled, there are as many as 32 free endosperm nuclei in the embryo sac. Kajale (1940b) reports their frequent crowding at the chalazal end. In *Amarantus retroflexus* (Dambroise, 1947) and *Psilostachys sericea* the free endosperm nuclei are uniformly distributed throughout the embryo sac (Fig. 35). Wall formation starts soon after the cotyledons appear. During the enlargement and maturation of the embryo most of the endosperm is consumed leaving only a few layers of cells in the mature seed (Fig. 36).

The first division of the oospore is transverse and subsequent similar divisions in the terminal as well as the basal cell result in a filamentous proembryo of six cells (Fig. 37). The lower three cells, *ci*, form a 6-10 celled suspensor which is uniseriate in the beginning but may become biseriate in the basal region (Figs. 38-40). Vertical divisions in the three cells, *l*, *l'* and *m*, result in a globular

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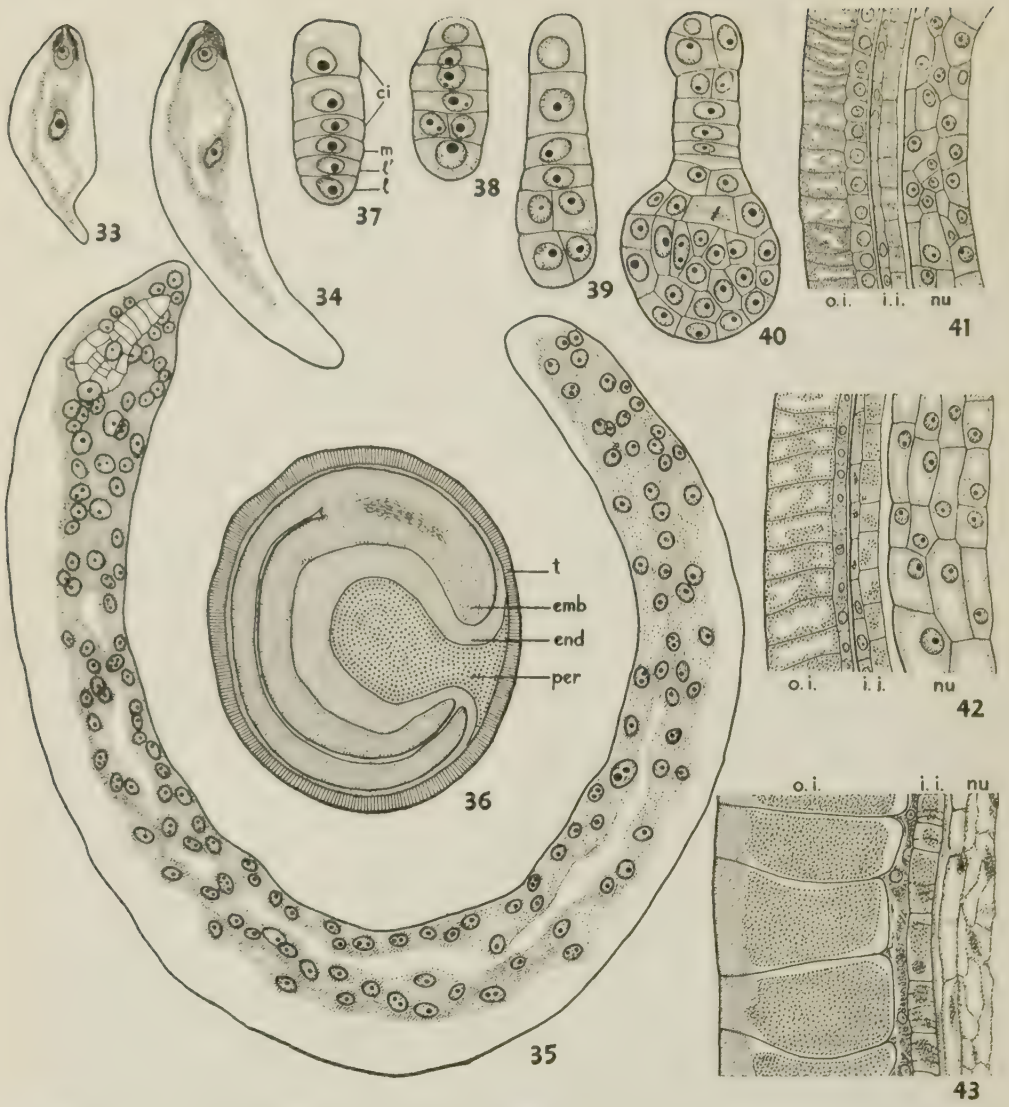
FIGS. 20-32 — Development of ovule and embryo sac. Figs. 20-23, l.s. carpel showing curvature of circinotropous ovule at megaspore mother cell, functioning megaspore and mature embryo sac stage. × 115. Fig. 24, l.s. young nucellus showing multicelled archesporium. × 1000. Fig. 25, megaspore mother cell with primary parietal cell divided anticlinally. × 1000. Fig. 26, linear tetrad of megaspores. × 1000. Fig. 27, functioning megaspore, note the three degenerated megaspores. × 1000. Figs. 28-30, two- and four-nucleate embryo sacs. × 1200. Fig. 31, mature embryo sac. × 1200. Fig. 32, abnormal nine-nucleate embryo sac. × 1200.



FIGS. 33-43 — Development of endosperm, embryo and seed coat. *t*=testa, *emb*=embryo, *end*=endosperm, *per*=perisperm, *o.i.*=outer integument, *i.i.*=inner integument and *nu*=nucellus. Fig. 33, origin of caecum at the base of the embryo sac, the antipodals have degenerated and disappeared. × 232. Figs. 34-35, enlargement of caecum, endosperm is free nuclear. × 232. Fig. 36, l.s. mature seed. × 32. Figs. 37-40, earlier stages in development of the embryo, for explanation see text. × 536. Figs. 41-43, development of seed coat. × 536.

mass from which arise the two cotyledons and the plumule. The embryogeny, therefore, resembles that of *Amarantus retroflexus* (Souéges, 1937b), *Alternanthera sessilis* and *Digera arvensis* (Joshi & Kajale, 1937) and corresponds to the 'Chenopodiad' type (Schnarf, 1931).

Seed Coat

Soon after fertilization the integuments undergo conspicuous changes. The outer layer of the outer integument elongates considerably, its outer wall becomes very thick and the cell cavities become filled

with tannin. The inner layer of the inner integument also enlarges slightly and becomes filled with tannin (Figs. 41-43). Towards the nucellus, a thin layer of cuticle is also secreted (Fig. 43). The two intervening layers, one belonging to the outer and one to the inner integument, are crushed and flattened in the mature seed. At the same time the embryo also enlarges and comes to lie closely pressed to the seed coat which is very hard and brittle and chips off while sectioning. This hardness is due to the thickness of the outermost wall of the seed coat. The thickening material stains green with safranin and fast green and appears to be hemicellulose.

Discussion

It is interesting to note that the family Amarantaceae portrays an assemblage of plants possessing several common features of floral morphology and embryology. In all its members the floral parts arise in acropetal succession. The flowers are minute, subsessile and comprise five perianth leaves, five stamens and two to three fused carpels. The ovary is unilocular and one-ovuled (except in the tribe *Celosieae*). In *Psilostachys sericea* each perianth segment receives three traces, each stamen one, and the gynaecium one ventral and two dorsal. *Digera arvensis* shows an almost similar vascular plan though there are contradictory reports about the vascular supply to its inner perianth leaves. While Hooker (1885) describes them as 2-4 nerved, Joshi and Rao (1934) find them to be univeined in the " few flowers " examined by them. This leads them to conclude that " the perianth of this plant, and of the family Amarantaceae in general, has been derived *totally by a modification of the stamens* " (italics mine) and that its ancestral form, therefore, had " naked flowers ". However, the single trace of the inner whorl of the perianth leaves of *D. arvensis* may have arisen either by a fusion of the three original traces or by a suppression of the two lateral ones. That this is more probable is supported by the presence of three veins even in the inner perianth segments of *Psilostachys sericea*. This is in accord with the views of Rendle (1903) who thinks that in typically monochlamydeous flowers with anti-perianth stamens, the perianth is " rather a protective foliar growth of the axis than a modification of the lower whorl of sporophylls ". The perianth in the Amarantaceae, therefore, appears to be foliar.

In the young anther lobe the archesporium is 1-4 cells across in transverse section. There is a single ephemeral middle layer. The cells of the glandular tapetum are 2-5 nucleate and secrete characteristic oily globules on the inner wall. When the tapetum degenerates the globules along with the unused tapetum come to lie on the endothecium. Kajale (1940a, b) thinks that they appear on the tapetum and later on the endothecium due to the disorganization of the inner walls of *both* these layers during microspore formation. The condition in *Psilostachys sericea* does not support such a view for there is no disorganization of the inner wall of the endothecium which develops the usual fibrous thickenings at maturity.

The pollen grains of *Alternanthera sessilis* and *Gomphrena globosa* are sculptured, in other genera they are psilate. The germ pores are cribellate throughout the family. Their number varies from six to many. Wodehouse (1935) characterizes the family as having 14 or more germ pores. This statement is obviously based on the study of the genus *Amarantus* only, and needs to be modified. The generative cell is lenticular. The mature pollen grain is mostly three-celled and the male cells are spindle shaped. At this time the tube nucleus puts up a degenerating appearance.

The ovule is crassinucellate and bitegmic. It is orthotropous to begin with but subsequent unequal growth causes it to curve, the curvature being of the extent of 360° in *Psilostachys sericea* and *Deeringia celosioides*. The inner integument forms the micropyle. Both the integuments are two layered and are separated by a wide air space at the chalazal end. In the Amarantaceae, *Digera arvensis* (Joshi & Rao, 1934; Puri & Singh, 1935) seems to be the only exception in not showing any such space.

Neumann (1935) attaches considerable importance to this air space from the taxonomic point of view and it is probable it may also be present in *D. arvensis*. A re-examination is necessary to settle this point.

The hypodermal archesporial cell cuts off a wall cell which may divide further but the parietal tissue is inconspicuous. A linear row of four megaspores is known in *Digera arvensis* (Joshi & Rao, 1934; Puri & Singh, 1935), *Allmania nodiflora*, *Cyathula tomentosa* (Kajale, 1940b) and *Psilostachys sericea*. In *Amarantus viridis*, *Pupalia lappacea* and *Aerua lanata*, Kajale (1940b) has recorded a row of three cells — two megaspores surmounted by a micropylar dyad cell. His conclusion is based on observations of the functioning megaspore with the other cells of the tetrad in such an advanced state of degeneration as to make it difficult to differentiate between adjacent cells. Stages similar to his Figs. 12*c* and 14*c* were observed several times in *Psilostachys sericea*. These were all mistaken, at first sight, for a row of two megaspores and the micropylar dyad. A closer observation, however, revealed the presence of a definite wall in the middle of the degenerating " dyad cell ". In Amarantaceae, therefore, a linear tetrad of four megaspores appears to be the rule rather than an exception and the occurrence of an undivided micropylar dyad may either be due to abnormality or faulty observation. The embryo sac development is of the ' Polygonum ' type.

The behaviour of the antipodal cells is variable. In *Psilostachys* they degenerate before the appearance of the embryo sac caecum. In others they appear to be more persistent (see Joshi, 1936; Kajale, 1935, 1937, 1940b). In *Pupalia lappacea* (Kajale, 1940b) they are said to divide until a mass of 30-40 cells is formed.

Self-pollination appears to be common. Fertilization is porogamous and usually results in the destruction of both the synergids. The pollen tube persists till about the eight-celled stage of the proembryo. It is a dead structure with no haustorial function whatever. Accessory pollen tubes are not infrequent. Joshi and Kajale (1937) state that in *Alternanthera sessilis* a pollen tube entered an embryo sac containing an eight-celled embryo. It appears probable, however, that the structure referred to as a fresh pollen tube may only be the persistent remnants of a tube which had entered earlier. It is not likely that an embryo already much past the fertilization stage can exercise any attraction for the pollen tube.

Soon after fertilization the embryo sac gives out a caecum which grows like a horse-shoe through the strongly curved nucellus some of which always persists as perisperm. The endosperm is free nuclear and the embryo of the ' Chenopodiad ' type. The suspensor is short and few celled. The structure of the seed coat has not been studied by the earlier authors but it is probable that it does not show any conspicuous variations from what has been described for *Psilostachys sericea*.

Summary

1. Each flower is subtended by a bract and two bracteoles. There are five imbricate perianth leaves. The bases of the five stamens are fused to form a short staminal tube and the gynaecium is bicarpellary syncarpous. The ovary is unilocular with a single circinotropous ovule. The style is hollow and the stigma bilobed.

2. The traces to the perianth, stamens and carpels arise in spiral succession. Each perianth leaf receives three traces which remain undivided, the stamens receive a single trace each and the gynaecium is supplied by one ventral and two dorsal traces.

3. The anther wall comprises the epidermis, fibrous endothecium, single ephemeral middle layer and the glandular tapetum. The microspore tetrads may be tetrahedral, isobilateral or decussate. At the time of shedding the psilate pollen grains are three-celled with six prominent cribellate germ pores.

4. The megaspores are arranged in a linear tetrad and the embryo sac is of the ' Polygonum ' type. The antipodals usually degenerate before the growth of the caecum.

5. Self-pollination appears to be common. During fertilization both the synergids degenerate. The pollen tube per-

sists till about the six-celled stage of the proembryo.

6. The primary endosperm nucleus divides prior to the division of the oospore and the endosperm is nuclear. Most of it is consumed by the growing embryo. Part of the nucellus persists as perisperm.

7. The development of the embryo is of the ' Chenopodiad ' type. The mature embryo is curved.

It gives me great pleasure to express my indebtedness to Prof. P. Maheshwari and Dr. B. M. Johri of the University of Delhi for their kind help in the preparation of this work. I am grateful to Mr. B. S. M. Dutt for the material, to Mrs. Martha Sinha for help in the translation of some French literature and to Principal M. L. Schroff and Dr. B. N. Mulay of my college for encouragement.

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FLORAL MORPHOLOGY AND SEED FORMATION IN *CUSCUTA REFLEXA* ROXB.

B. M. JOHRI AND B. TIAGI
University of Delhi, Delhi, and Government College, Ajmer, India

All species of *Cuscuta* investigated so far show a monosporic embryo sac of the Polygonum type (see Peters, 1908; Macpherson, 1921; Fedortschuk, 1931; Smith, 1934; Tiagi, 1951). The only exception is *C. reflexa* in which Johri and Nand (1934) reported an Allium type. Finn (1937) and Maheshwari (1941) have suggested a rechecking of this species. Maheshwari says that " such a difference is possible but not so probable, and it seems that Johri and Nand's observations need confirmation ".

There seems to be much variation in the development of the embryo and suspensor. The species of the subgenus *Eucuscuta* show a multicellular suspensor of uninucleate cells (Peters, 1908; Fedortschuk, 1931; Tiagi, 1951) while in the subgenus *Monogyna* the suspensor consists of a few vesicular coenocytic cells (Fedortschuk, 1931; Johri, 1951).

Material and Methods

Cuscuta reflexa is found throughout India and parasitizes a large number of plants. It flowers from September to April. Plants were grown on *Adhatoda vasica* in the botanic garden of the Government College, Ajmer. Some material was also collected from Agra[1], Ghaziabad and Delhi. Buds, flowers and fruits were fixed in formalin-acetic-alcohol. The ovary wall as well as older ovules were trimmed on two parallel sides to facilitate infiltration. The usual methods of dehydration and embedding were followed. Sections were cut 8-15 μ thick and stained in iron-haematoxylin as well as in safranin and fast green. The latter combination proved more satisfactory. Several slides stained by one of us (B.M.J.) in 1934 in crystal violet and erythrosin were satisfactory even at the time of this study. Smear preparations stained with acetocarmine were also examined.

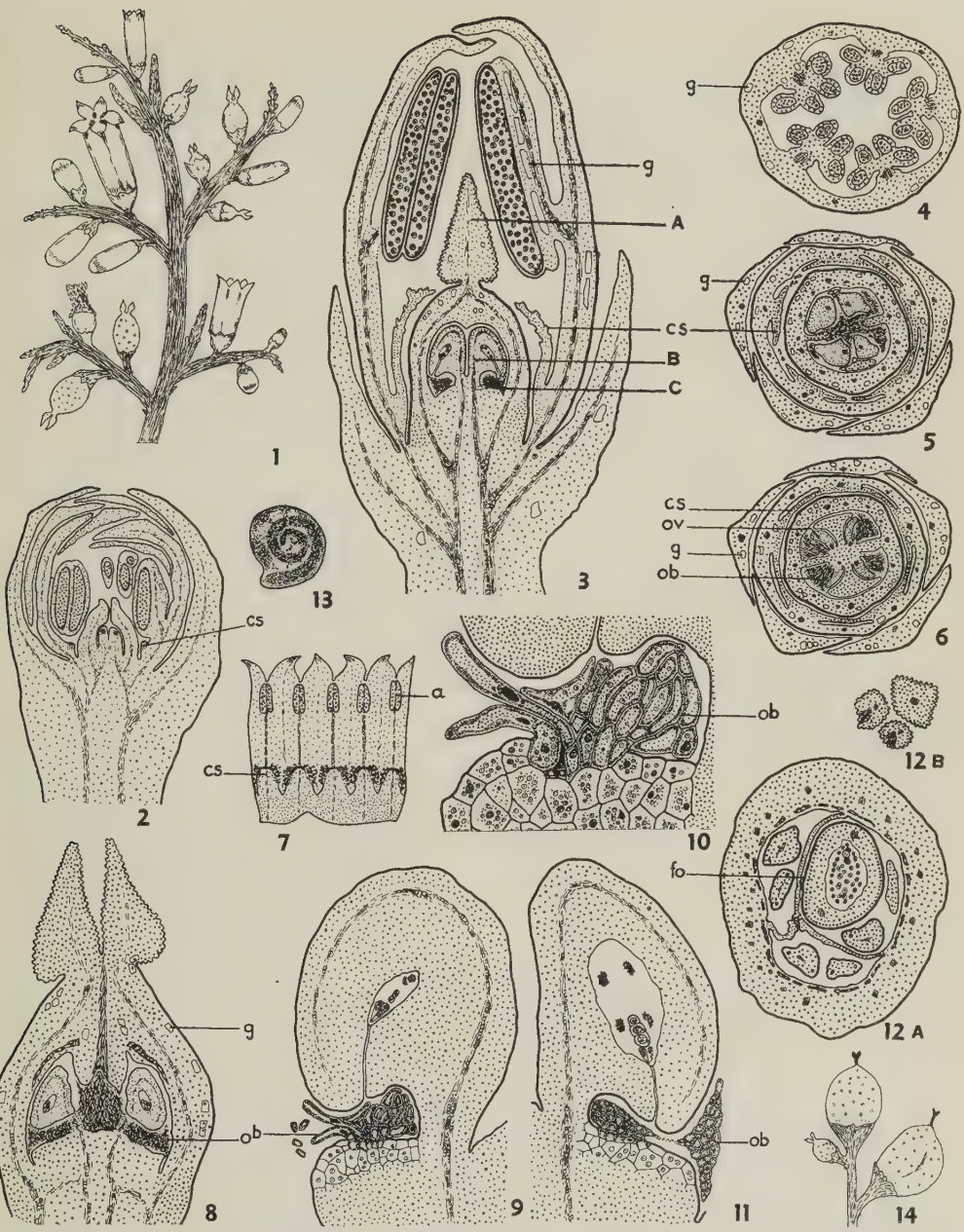
1. We are obliged to Prof. Bahadur Singh and Shri R. L. Paliwal of B. R. College, Agra, for sending some fixed material of *Cuscuta reflexa* from Agra.

The Flower

The whitish-yellow, bracteate and subsessile flowers are arranged in bunches (Fig. 1). The floral organs arise in acropetal succession. Five fleshy sepals, slightly fused at the base, are followed by a campanulate corolla of five segments with reflexed apices. Five oblong, four-celled, epipetalous anthers are inserted on short filaments in the throat of the corolla (Figs. 2-4). Richly protoplasmic gum cells and starch grains occur in all floral organs.

At the base of the corolla tube and immediately below the anthers arises a corona consisting of five fimbriate scales (Figs. 3, 5-7; *cs*). It is initiated at the time of differentiation of the nucellar archesporium (Fig. 2), is well developed at the four-nucleate embryo sac stage (Fig. 3) and shrinks soon after fertilization. It is devoid of any vascular trace. Hooker (1885), Duthie (1911), Rendle (1925), Fernald (1950); and Clapham, Tutin and Warburg (1952) refer to these appendages as ' scales ' although Rendle states that they recall the corona of the Boraginaceae.

The gynaecium is usually bi- but sometimes tricarpellary, with a globose ovary, a short style or none, and two or three lanceolate papillose stigmas (Figs. 2, 3, 8, 12A, 12B). The ovary is two-celled, occasionally three-celled, but the septum does not reach up to the base and each locule has two ovules on a basal axile placenta (Figs. 5, 8, 12A).



FIGS. 1-14 — Floral morphology. Fig. 1, part of inflorescence showing buds, flowers and fruits. × 1. Figs. 2, 3, l.s. buds at archesporial and four-nucleate embryo sac stage. × 19. Figs. 4-6, cross-sections of flower at levels 'A', 'B' and 'C' respectively in Fig. 3. × 10. Fig. 7, corolla tube opened to show corona and anthers. × 2·5. Fig. 8, l.s. ovary showing disposition of obturators. ×19. Fig. 9, single ovule with placental obturator. × 57. Fig. 10, obturator enlarged. × 132. Fig. 11, obturator being crushed by enlargement of ovule. × 57. Fig. 12, t.s. of a tricarpellary ovary (A) and stigma (B) with only one ovule maturing. × 10. Fig. 13, mature seed. × 2·5. Fig. 14, fruits. × 1. (*a*, anther; *cs*, coronary scale; *fo*, fertile ovule; *g*, gum cell; *ob*, obturator; *ov*, ovule.)

The upper part of the placenta adjacent to the funiculus proliferates to form four glandular obturators (Fig. 6) which become almost continuous slightly higher up where they meet the septum (Figs. 5, 8). The obturator is in close proximity to the micropyle and its mucilaginous cells are very conspicuous at the time of fertilization (Figs. 9, 10). Probably it provides nourishment to the growing pollen tubes. Subsequent growth of the ovule during embryo formation crushes the obturator (Fig. 11).

Usually only a single ovule in each ovary develops into a seed while the others abort (Fig. 12A). The shrivelled reniform seed has a hard testa and the coiled embryo is not differentiated into cotyledons (Figs. 13, 107). The fruit is a circumscessile capsule which ruptures from the base (Fig. 14).

Microsporogenesis and Male Gametophyte

Microsporogenesis and development of the male gametophyte proceed in the usual way as described earlier by Johri and Nand (1934). Tiagi (1951) has recently made similar observations in *Cuscuta hyalina* and *C. planiflora*. Some additional information regarding tapetum, male gametophyte, polyspory, compound pollen grains and development of pollen grains in the ovary wall of *C. reflexa* are presented here.

Before the microspore mother cells enter Meiosis I, the tapetal nuclei divide so that the cells become binucleate. During Meiosis II some of them may show even three nuclei (Fig. 15). They take a dull stain and are poor in chromatin but show several nucleoli. During the organization of the microspore tetrads the tapetal nuclei become hypertrophied and fuse irregularly (Figs. 16, 17). Fedortschuk (1931) and Tiagi (1951) report two-nucleate tapetal cells in *C. monogyna* and *C. hyalina* respectively. According to the first author, in *C. epithymum* as many as four nuclei may be present which fuse to form a common mass.

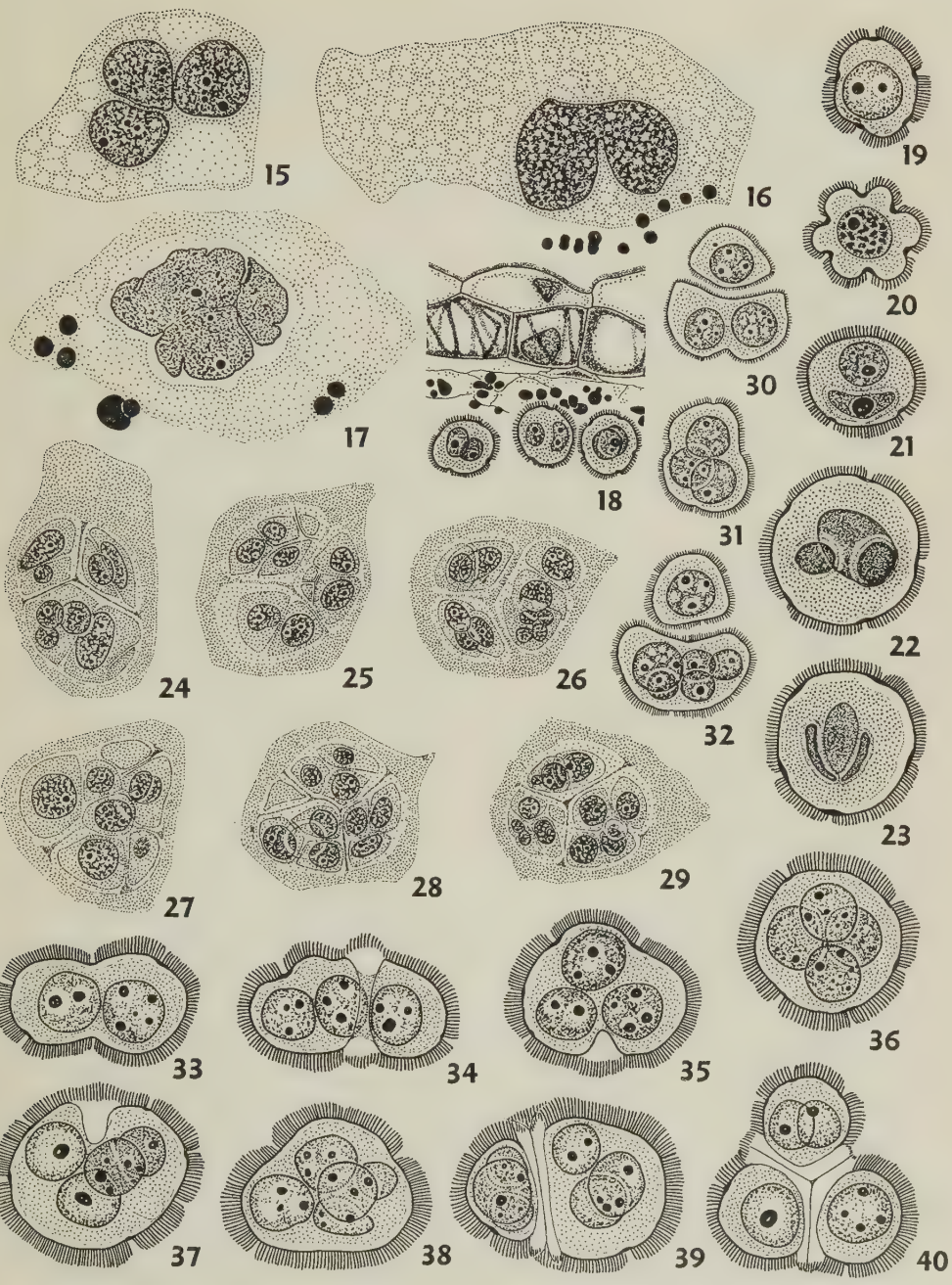
While the pollen grains are still uninucleate, oily globules appear on the inner side of the tapetal protoplasts (Figs. 16-18). It is probable that they may contribute to the formation of the exine. The tapetum shows signs of degeneration when the pollen grains are bicelled and at the same time fibrous thickenings appear in the endothecium (Fig. 18).

The pollen gains are spherical and show five germinal furrows (Fig. 19) although frequently four or six may be present (Fig. 20). The tube and generative nuclei are almost of the same size but subsequently the latter elongates (Fig. 21). Finn (1937) reports that in *C. monogyna* the spindle-shaped generative cell extends throughout the entire breadth of the pollen grain so that it touches the intine on either side. In *C. reflexa* there is no such pronounced extention. On division, the generative cell gives rise to two spherical sperm cells which later become elongated (Figs. 22, 23).

Polyspory — A number of microspore " tetrads " showed as many as 10-11 microspores and occasionally two, three or four nuclei were present in some of the microspores (Figs. 24-29). This is due to supernumerary divisions in one or more of the four microspores with or without the accompaniment of wall formation. All the microspores are thus not of the same size and the nuclei of the multinucleate microspores also show some variation (Figs. 24-29). Polyspory was observed only in one pollen sac of a single anther. Two pollen sacs of the same anther had uninucleate pollen grains of two sizes — normal and smaller — and the third showed microspore mother cells undergoing normal reduction divisions.

Polyspory is already known in a number of other plants. Beer (1906) observed six to ten microspores in *Fuchsia*, Shoemaker (1926) noted six in a variety of apple called " Stayman Winesap " and Penland (1923) saw as many as ten to twelve in *Rosa*. *Atraphaxis* (Edman, 1931) and *Coffea* (Krug and Mendes, 1940) also show a similar condition (for references see Maheshwari, 1949). Anzalone (1949) reports " polyads " (= polyspores) in *Taraxacum megalorrhizon* which is a tetraploid apomict.

Multinucleate Pollen Grains — In Figs. 30-32 one of the microspores shows two, three and five nuclei respectively.



FIGS. 15-40 — Microsporogenesis and male gametophyte. Figs. 15-17, tapetal cells showing multinucleate condition and fusion of nuclei, note oily globules on inner side represented by large black dots. × 715. Fig. 18, epidermis, fibrous endothecium, degenerated tapetum and bicelled pollen grains × 359. Figs. 19, 20, uninucleate pollen grains with five and six germinal furrows respectively. × 715. Fig. 21, bicelled pollen grain. × 715. Figs. 22, 23, three-celled pollen. × 715. Figs. 24-29, tetrads with more than the usual number of microspores some of which are multinucleate. × 715. Figs. 30-32, uni- and multinucleate microspores. × 715. Figs. 33-38, multinucleate pollen grains. × 715. Figs. 39, 40, two and three microspores fused to form compound pollen grains; in the former both the cells are trinucleate while in the latter one is binucleate. × 715.

The pollen grains represented in Figs. 33-38 show two, three, four or five nuclei lying in a common cytoplasm. It is likely that they have originated from a multinucleate microspore of the type referred to above. Two other possibilities suggest themselves: (a) the single nucleus of the pollen grain may have divided and redivided as has been reported in *Hyacinthus* (Stow[2], 1930) and *Zea mays* (Beadle[2], 1931), or (b) there may have been a failure of wall formation during meiosis as in *Kniphofia* (Moffett, 1932). Microspore " tetrads " of this second type have not actually been observed but such a course is suggested by Figs. 34, 35 and 37 in which the furrows have been arrested before completion. Figs. 39 and 40 represent cases in which two and three microspores respectively are still attached together. Both the cells in the former are three-nucleate but one cell is much larger than the other, while in Fig. 40 all the three cells are of equal size and only one of them is binucleate. The multinucleate condition may have originated in the tetrad itself or at a later stage.

The multinucleate and the normal uninucleate pollen grains occur in the same pollen sac but the former are several times larger. Their nuclei are of about the same size except in a few cases (cf. Fig. 19, Figs. 33-38). In Fig. 38 one of the four nuclei seems to have undergone the third division.

The occurrence of polyspory and compound pollen grains in *Cuscuta* must be considered as an abnormality rather than an usual feature since out of over a thousand flowers examined, only a few showed such irregular development. However, there is considerable sterility in the pollen grains many of which do not proceed beyond the two-celled stage at the time of shedding and stain very deeply.

Fedortschuk (1931) has observed compound pollen grains in *Cuscuta epithymum* showing the following: two vegetative nuclei; two vegetative nuclei and the generative cell dividing; one vegetative nucleus and three sperm cells; one vegetative nucleus, two sperm cells and a prothallial cell. There was also seen a pollen grain with two separate protoplasts — one with a vegetative nucleus and the other with the vegetative as well as the generative cell. No instance of the occurrence of a prothallial cell has been seen in *C. reflexa*.

Pollen Grains in the Ovary Wall — In two cases a part of the ovary wall near the stigmatic region was found to have become sporogenous and differentiate into microspore mother cells (Figs. 41, A; 43), and even microspores (Figs. 42, B; 44). Whether they can reach maturity and bring about pollination and fertilization could not be determined. The oily globules on the inner side of the tapetum and fibrous thickenings in the hypodermal layer gave the appearance of a normal pollen sac except for three middle layers instead of one. The flower showing microspore mother cells in the ovary wall had two-celled pollen grains in the anthers. In the second flower the anthers had been removed before fixation.

Megasporogenesis and Female Gametophyte

The unitegmic tenuinucellate ovule becomes anatropous by the time the four-nucleate embryo sac is formed (Fig. 3). The single massive integument invests the scanty one-layered nucellus which is consumed by the enlarging embryo sac. The cells of the integument, especially those forming the two innermost layers, are full of starch but an endothelium does not differentiate. During further growth the embryo sac encroaches upon the integument and its apical part reaches up to the base of the micropyle. The vascular trace entering the funiculus extends up to the apex of the integument on the distal side (Figs. 9, 11).

2. Quoted from Moffett (1932).

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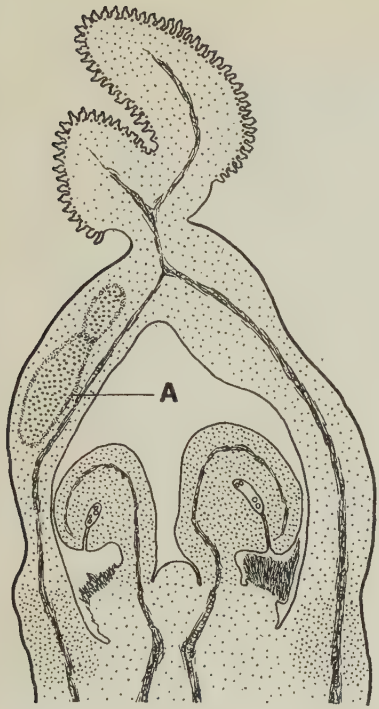
Figs. 41-44. Figs. 41, 42, l.s. abnormal ovaries showing site of differentiation of microspore mother cells and pollen grains at 'A' and 'B' respectively. × 41. Figs. 43, 44, portions of 'A' and 'B' enlarged; note the binucleate tapetum in the former and fibrous endothecium in the latter. × 283.



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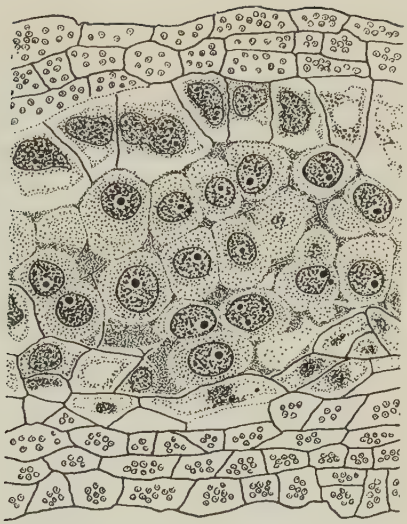

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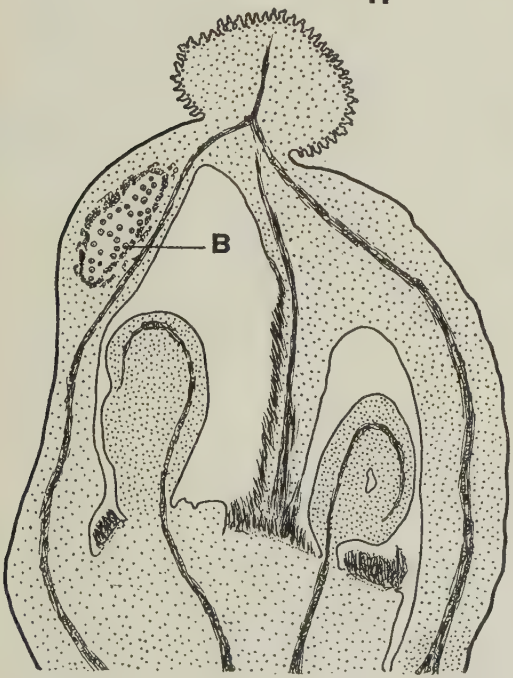

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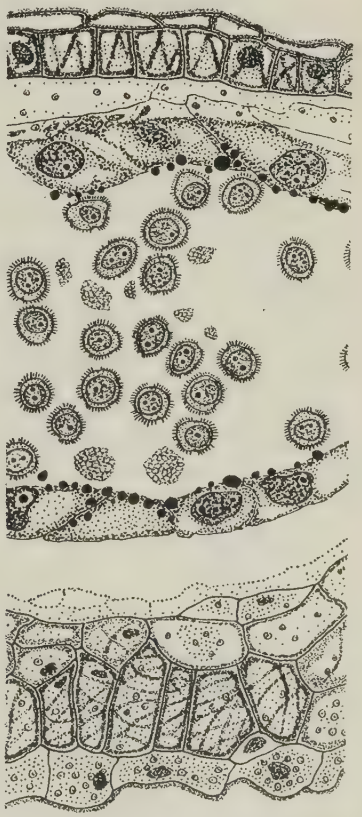

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FIGS. 41-44.

Usually a single hypodermal archesporial cell differentiates in the nucellus and functions directly as the megaspore mother cell (Fig. 45). Occasionally two megaspore mother cells may develop in the same nucellus (Fig. 46). The first division gives rise to a dyad of two almost equal cells (Figs. 47, 48). The lower dyad cell enlarges and divides (Figs. 49, 50) but since no cell-plate is laid down, this results in a two-nucleate embryo sac (Fig. 51). In the meantime, the upper dyad cell has degenerated without undergoing any division (Figs. 49-51). Two further divisions of the two-nucleate embryo sac lead to the eight-nucleate stage (Fig. 52). The antipodal cells are usually ephermeral and degenerate before fertilization (Fig. 53). The synergids have long beaks and become vacuolated only at a late stage (cf. Figs. 52, 53). Starch is abundant in the egg apparatus and general cytoplasm of the embryo sac. The development is, therefore, bisporic and conforms to Allium type.

Abnormal Embryo Sacs—If two megaspore mother cells function simultaneously in the same nucellus, they can give rise to two embryo sacs as shown in Fig. 54. In case the intervening wall between the embryo sacs disappears, all the nuclei come together and organize in a different way. In Fig. 55 there are two egg apparatuses and three polar nuclei; the antipodals had presumably degenerated and were not seen. The fourth polar nucleus could not be traced and it is possible that one of the three nuclei is a fusion product although this is rendered improbable by the similar size of all the three. Fig. 56 shows an embryo sac with a single synergid and the egg besides the four free nuclei in the centre. It has not been possible to interpret it with certainty but one of the synergid nuclei may have moved down and one of the antipodals may have moved up giving rise to the group of four. The other two antipodals may have degenerated. The embryo sac in Fig. 57 shows two synergids, two eggs, an irregularly lobed nucleus formed by the fusion of six (?) nuclei, and six free nuclei lying lower down. We consider that these last represent the antipodal nuclei which have moved up and escaped degeneration, and that the two nuclei which should normally have organized into synergids have fused with four polar nuclei to form the large-lobed nucleus with five large and three smaller nucleoli.

Fertilization and Polyembryony

As the pollen tube enters the embryo sac, it demolishes one of the synergids but its nucleus may sometimes persist. Double fertilization was not actually observed but may be presumed to occur normally. Remnants of the pollen tube persist during earlier stages of embryogeny (Figs. 60, 71, 74, 79, 91).

An unusual feature is the persistence of one of the synergids which enlarges after fertilization and becomes very prominent (Figs. 71-74, 76, 78-80, 82, 85, 87-91, 94-97). It can be recognized until the proembryo has elongated and the stem tip has differentiated (Fig. 64). In Fig. 90 the synergid occupies a lateral rather than the terminal position because the proembryo has slightly pushed into the

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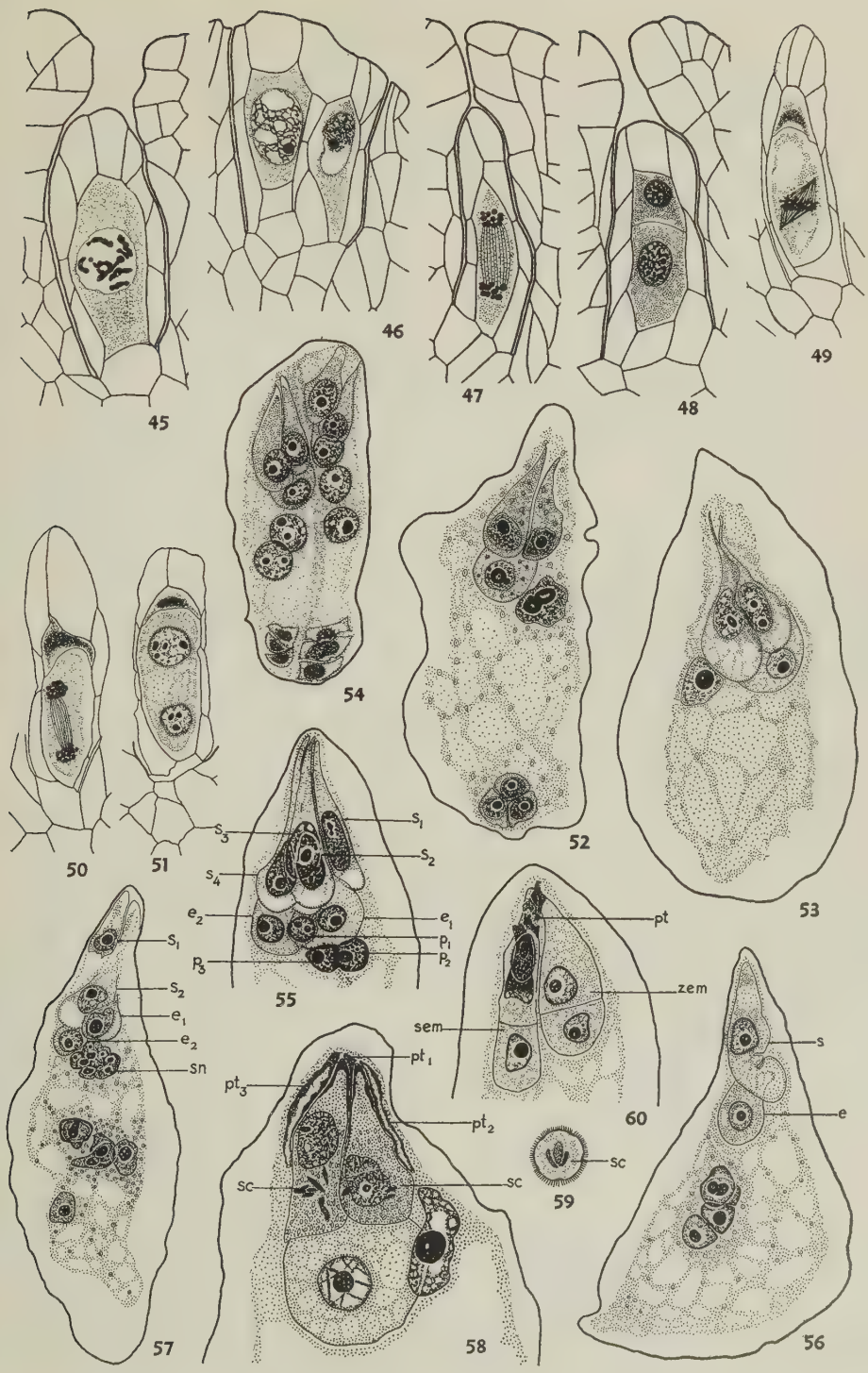
Figs. 45-60 — Megasporogenesis, female gametophyte and fertilization. Fig. 45, part of ovule showing megaspore mother cell and massive integument. × 404. Fig. 46, two megaspore mother cells in same nucellus. × 404. Fig. 47, early telophase of Meiosis I. × 404. Fig. 48, dyad. × 404. Figs. 49, 50, lower dyad cell in metaphase and telophase respectively; upper dyad cell degenerating. × 404. Fig. 51, two-nucleate embryo sac. × 404. Fig. 52, mature embryo sac; note starch grains in egg apparatus and general cytoplasm. × 404. Fig. 53, same with polars fused and antipodals degenerated. × 264. Fig. 54, twin embryo sacs. × 404. Fig. 55, compound embryo sac with two egg apparatuses and three other nuclei. × 264. Figs. 56, 57, abnormal embryo sacs: for explanation see text. × 264. Fig. 58, unusual case of fertilization; note remnants of three pollen tubes and 10-11 sperm cells. × 264. Fig. 59, mature pollen grain; compare shape and size of male cells with those of Fig. 58. × 264. Fig. 60, embryo sac showing two bicelled proembryos, one developed from the oospore and the other from a synergid. × 264. (*e*, egg; *p*, polar; *pt*, pollen tube; *s*, synergid; *sc*, sperm cell; *sn*, secondary nucleus; *sem*, synergid proembryo; *zem*, zygotic proembryo.)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FIGS. 45-60.

micropyle and displaced the synergid. Fedortschuk (1931) reports that the nucleus of the persisting synergid had once divided in *C. monogyna*, but we did not come across any such case in *C. reflexa*. We are inclined to think that in her Fig. 17 (*C. monogyna*) what she represents as a synergid (S_1) may well be the tip of the pollen tube as also indicated by its shape and contents (cf. our Figs. 60, 71, 74, 79, 91).

Occasionally when an embryo sac fails to be fertilized, it continues to enlarge and the egg apparatus reaches an abnormal size. In two such cases the wall of the synergids had thickened considerably and taken a bright green colour with safranin and fast green (cf. Fedortschuk's Fig. 17A of *C. monogyna*).

A very unusual case of fertilization is shown in Fig. 58. The oospore has enlarged considerably and the primary endosperm nucleus is lying adjacent to it. Three sperm cells are lying just over the nucleus of one synergid and seven (or eight) over or in the other synergid below its nucleus. The size and shape of the sperm cells is quite comparable with that of the sperm cells in a normal pollen grain drawn at the same magnification (Fig. 59). Three pollen tubes appear to have entered this embryo sac (Fig. 58; pt_1, pt_2, pt_3). The number of sperm cells, however, is larger than three pollen tubes could have normally discharged. Possibly some of the pollen tubes carried more than two sperm cells each — a condition resulting from supernumerary divisions of the two sperm cells in the pollen grain (see also Fedortschuk, 1931) or the pollen tube or after their discharge. That one of the synergids may be fertilized in such cases is suggested by Fig. 60 which shows two bicelled proembryos, one zygotic and the other derived from a synergid. The latter shows remnants of the pollen tube at its apex. It could not be determined if a second pollen tube also entered this embryo sac. If it did not, it is probable that the first pollen tube contained more than two sperm cells, one of which may have fertilized the synergid or possibly the synergid developed parthenogenetically. In adjacent sections, the above embryo sac showed the other synergid and two endosperm nuclei.

Polyembryony has not been observed in any other species of *Cuscuta* but Macpherson (1921) reports synergid embryos in *Convolvulus sepium*.

Endosperm

After fertilization the embryo sac continues to expand and consume the adjacent cell layers of the integument. The primary endosperm nucleus divides at about the same time as the oospore, but occasionally it may divide earlier (Fig. 61). One embryo sac showed eight endosperm nuclei while the oospore was still undivided. Fig. 62 shows a two-celled proembryo and only two endosperm nuclei. The number of the endosperm nuclei may increase up to ten or more at this stage. As a rule they divide simultaneously but occasionally some may lag behind and these may be distinguished by their larger size. The number continues to increase and when the proembryo is three-celled, there may be twenty to fifty nuclei (Fig. 63). Finally, when a much larger number has been formed, they take up a peripheral position and cell formation is initiated. The endosperm tissue around the proembryo soon becomes cellular and wall formation gradually progresses inwards filling up the entire embryo sac (Figs. 64, 65). The endosperm cells have very thin walls and

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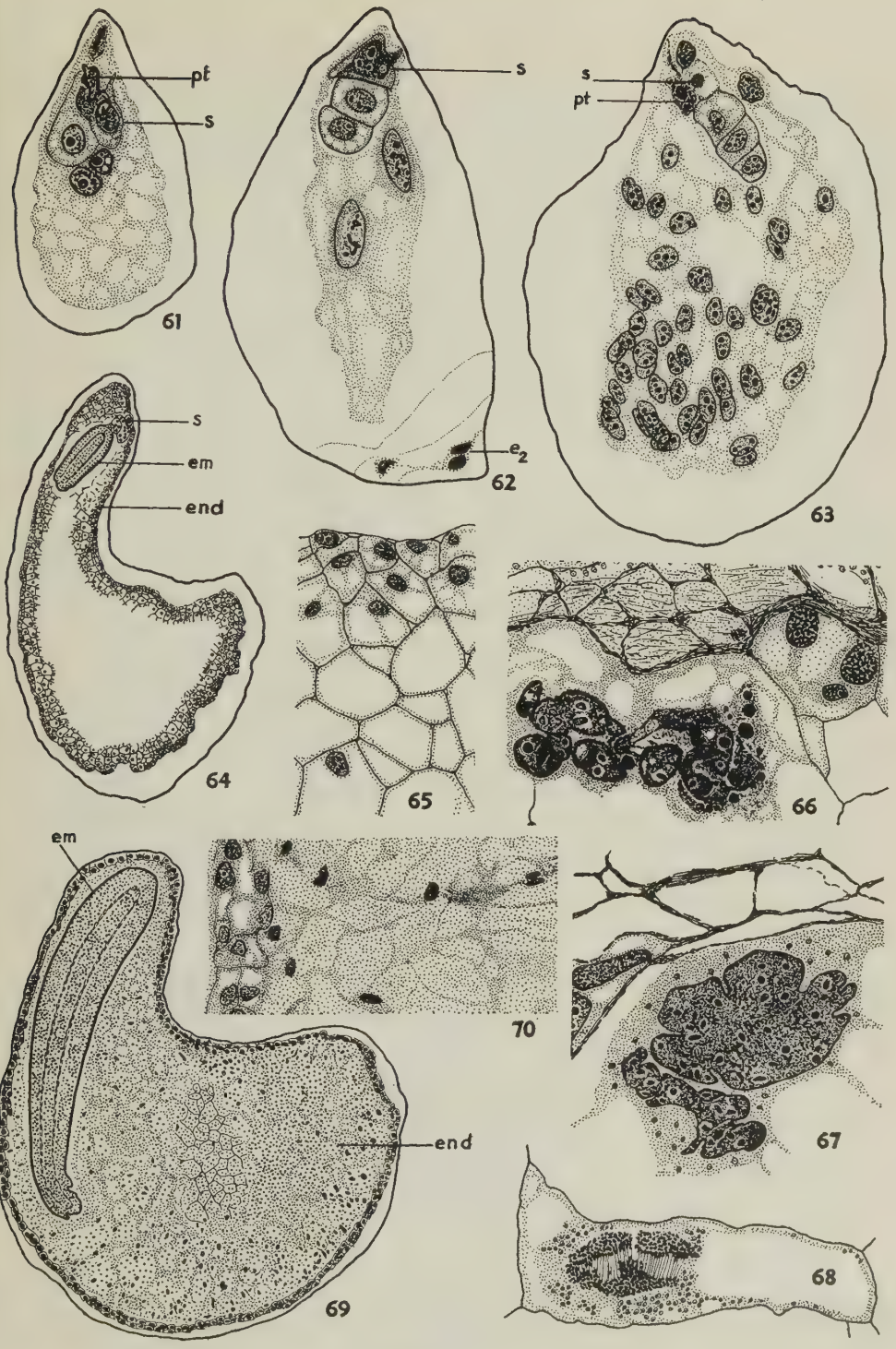
FIGS. 61-70 — Endosperm formation. Fig. 61, embryo sac showing two endosperm nuclei, undivided oospore and one persisting synergid. × 204. Fig. 62, bicelled proembryo and two endosperm nuclei; note another degenerated embryo sac e_2 at base. × 204. Fig. 63, three-celled proembryo with approximately 50 endosperm nuclei. × 204. Fig. 64, cellular endosperm. × 15. Fig. 65, part of cellular endosperm enlarged. × 204. Figs. 66, 67, endosperm cells adjacent to integument showing aggressive activity; note formation of polyploid nuclei. × 296. Fig. 68, mitotic division of polyploid endosperm nucleus. × 296. Fig. 69, gelatinization of inner endosperm tissue to form a mucilaginous matrix. × 15. Fig. 70, part of mucilaginous matrix enlarged to show remnants of cell walls and nuclei. × 204. (*em*, embryo; *end*, endosperm; *pt*, pollen tube; *s*, haustorial synergid.)



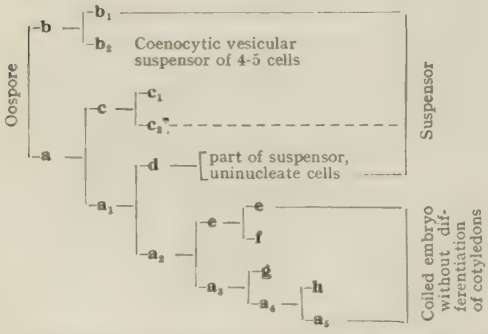
FIGS. 61-70.

do not contain much reserve food. As the proembryo elongates and the stem tip is differentiated, the central endosperm tissue gelatinizes to form a homogeneously staining mucilaginous matrix (Figs. 69, 70). At the same time the walls of peripheral cells of the endosperm break down and the nuclei seem to become free and fuse irregularly (Figs. 66, 67). They are surrounded by dense cytoplasm and the polyploid nuclei divide mitotically (Fig. 68). In the mature seed the mucilaginous remnants of the endosperm surround the embryo and occupy the spaces between its coils (Fig. 108).

Embryo

Fedortschuk (1931) has pointed out that two different types of suspensor cells are formed in the embryos of *C. monogyna* and *C. epithymum* respectively. From the following description it would be evident that both these types occur in *C. reflexa* and even intermediate stages are found.

The oospore enlarges and divides transversely to produce the basal cell *b* and the terminal cell *a* (Fig. 71). The terminal cell and its derivatives divide by transverse walls to produce the cells *c*, *d*, *e*, *f*, *g*, *h* and a_1-a_5 (Figs. 72-81, 91-97). The sequence of divisions of the oospore and its daughter cells and their ultimate fate in the formation of the embryo is as follows:



The cell *c* may divide longitudinally when the proembryo is only three-celled (Fig. 73). The basal cell *b* mostly remains undivided (Figs. 72-76, 78-80, 83, 88-90) but sometimes it divides longitudinally (Figs. 77, 81, 82) or even transversely (Figs. 84, 85). The cell *c* also behaves very much like the basal cell. It may remain undivided (Figs. 76, 78, 80, 81) or divide longitudinally (Figs. 75, 77, 79, 83, 84) or transversely (Fig. 85). In Fig. 82 the cell *c* has undergone two longitudinal divisions while in Fig. 86 it seems to have produced there daughter cells. The cells *b* and *c* and their derivatives form a characteristic suspensor. Its cells enlarge considerably, become vesicular, vacuolated and multinucleate. The nuclei divide repeatedly and as many as seventy may be counted in the undivided basal cell *b* in Fig. 83. Their number, however, is reduced as the result of nuclear fusions (Figs. 79, 80, 82, 84, 86-90). Fedortschuk (1931) has made similar observations in *C. monogyna* but she considers that the cells *b* and *c* remain undivided.

The cell *d* divides longitudinally and transversely giving rise to two tiers of cells (Figs. 78-85, 88). They also become vacuolated and their staining reaction is similar to that of suspensor cells. They may, therefore, be considered to be a part of the suspensor as is also borne out by their subsequent behaviour (Figs. 86, 99, 101). These cells do not become vesicular or multinucleate but often protrude into the adjacent coenocytic suspensor cell. According to Fedortschuk, in *C. monogyna* the cell *d* produces two tiers of two cells each. First the longitudinal wall between the two cells of the upper tier dissolves and the binucleate cell pushes into the adjacent suspensor cell. The cells of the lower tier behave likewise. These cells may also enlarge and become multinucleate like the other

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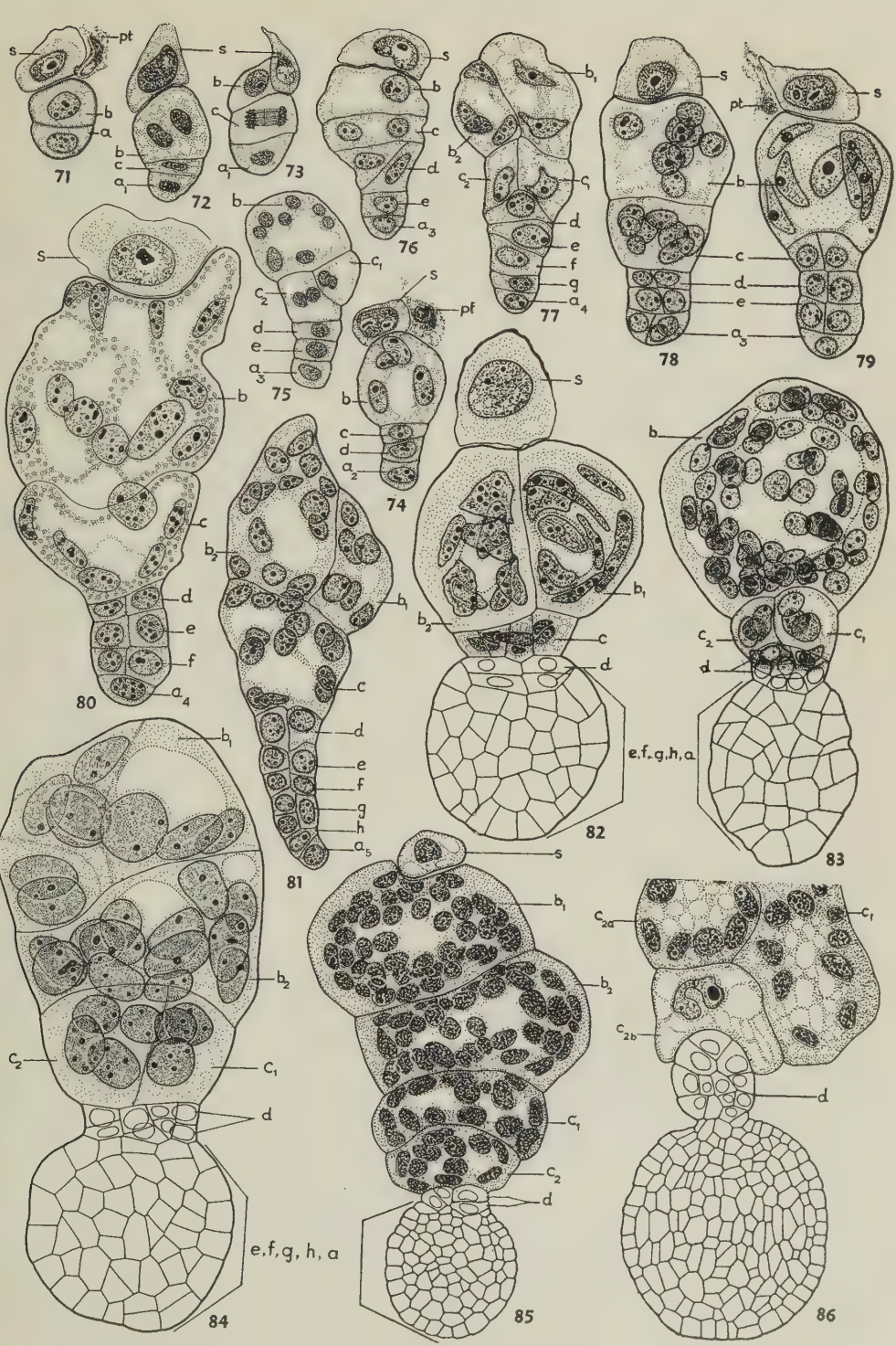
FIGS. 71-86 — Development of proembryo. Figs. 71-81, sequence of divisions in the terminal cell of the bicelled proembryo to establish the tiers *d*, *e*, *f*, *g*, *h* and a_1-a_5; note the formation and disposition of vesicular coenocytic suspensor cells b_1-b_2 and c_1-c_2, also c_{2a} and c_{2b} in Fig. 86. × 248. Figs. 82-84, formation of embryonal mass from the cells *e*, *f*, *g*, *h* and *a*; the cell *d* gives rise to two tiers of cells. ×248. Figs. 85, 86, same, advanced stage. × 121. Note the haustorial synergid *s* in Figs. 71-74, 76, 78-80, 82, 85 and remnants of the pollen tube *pt* in Figs. 71, 74, 79.



FIGS. 71-86.

suspensor cells. We are, however, unable to confirm these observations in *C. reflexa*. None of the walls of the two tiers of cells derived from the cell *d* show any signs of dissolution (Figs. 80-86), and it is unlikely that they would become vesicular and coenocytic.

The variations of the suspensor in *C. reflexa* may now be taken up. Considering the size of the proembryo, Figs. 87-90 show a comparatively reduced type of suspensor (cf. Figs. 80-86). Figs. 91-97 represent a series of proembryos in which the suspensor consists of uninucleate cells only. This condition resembles that of *C. epithymum* (Fedortschuk, 1931). It is interesting to note that in *C. reflexa* embryos with both the types of suspensor may occur in the same ovary.

The cells *e, f, g, h* and a_5 divide irregularly and produce a globular mass of cells (Figs. 81-90) which elongates considerably. The stem tip differentiates at the distal end and vascular strands make their appearance. A root cap is not formed (Figs. 98-101). The suspensor, including derivatives of the cell *d*, disorganizes and forms a shapeless mass (Fig. 101) which is absorbed. Elongation of the embryo continues without any differentiation of the cotyledons and for lack of space it coils on itself (Figs. 102-108). The coiling may sometimes be irregular (Figs. 103, 106). The vascular strands of the embryo do not show any distinction into xylem and phloem. The stem tip has several spirally arranged scales (Figs. 105, 107). Their exact morphology is not understood but they may be in the nature of protective structures around the stem tip. Macpherson (1921) observed two small scales near the apex of the embryo in *C. gronovii* and according to her neither of these scales can be considered as a cotyledon. Fernald (1950) also refers to plumular scales in *Cuscuta*.

Seed and Fruit

Seed Coat — At the time of fertilization the integument comprises approximately fifteen layers of parenchymatous starchy cells (Fig. 109). In the region of the funiculus it is considerably thicker. The vascular strand with well-formed tracheides runs all round the integument close to its outer margin. The innermost four or five layers adjacent to the embryo sac look famished and are soon crushed by its enlargement.

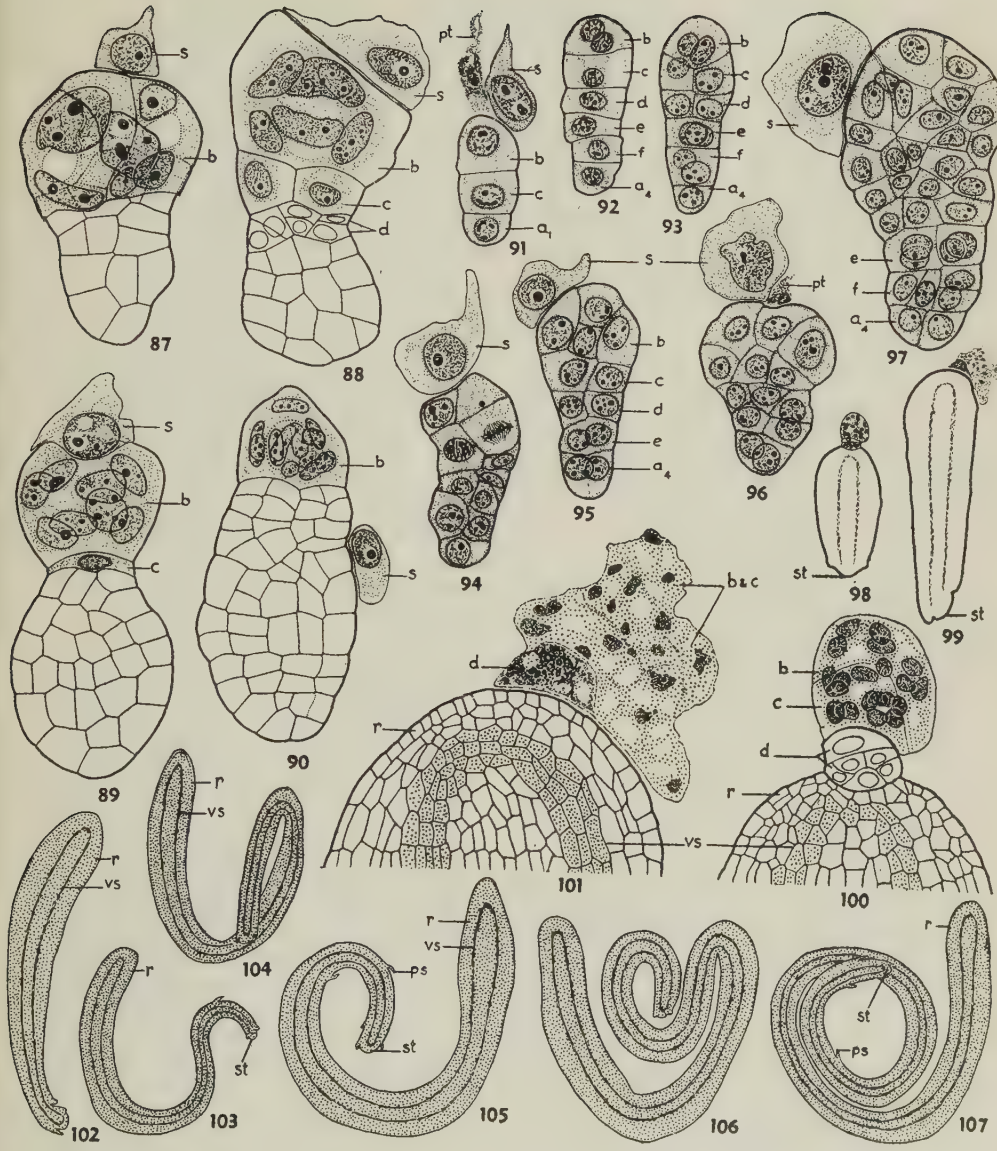
By the time proembryo is advanced (Fig. 86) the outer wall of the integumentary epidermis becomes thick, the hypodermal layer remains narrow and thin-walled, the second layer elongates and cells of the second and third hypodermal layers become prominently lignified (Figs. 110, 111). In the funicular portion the cells of the epidermis and hypodermis also elongate and get lignified. Consequently the seed coat becomes very hard and the seeds are difficult to section.

While these changes are going on in the outer part of the integument, cell formation is initiated in the peripheral part of the endosperm. The cells adjacent to the integument become very aggressive (Figs. 66, 67) and invade the latter gradually consuming all the parenchymatous starchy layers (cf. Figs. 109-111) excepting one or two around the vascular strand. At this stage the embryo has reached maturity and completely fills up most of the space (Fig. 108). At places the epidermis of the testa peels off due to the breaking down of the thin-walled narrow hypodermis and, therefore, it consists of only two lignified layers of cells with crushed remains of other layers followed by a layer of endosperm.

Pericarp — Even before fertilization, one to two hypodermal layers of the inner ovary wall and a group of cells at the base of the style become prominently lignified (Figs. 112, 113). As the ovules enlarge, the inner wall of the ovary is crushed and the thickened layers, which also break down, are pushed up. The outer epidermis of the ovary wall is thick and cuticularized. When the seeds are ripe, an abscission layer at the base of the ovary brings about a circumscessile dehiscence.

Degeneration of Ovules and Sterility

Occasionally either the oospore or only the primary endosperm nucleus may



Figs. 87-107. Figs. 87-90, proembryos with reduced vesicular coenocytic suspensor cells. × 248. Figs. 91-97, proembryos without vesicular suspensor. × 248. Figs. 98, 99, advanced embryos with stem tip differentiated. × 24. Figs. 100, 101, enlargement of radicular ends of the embryos shown in Figs. 98, 99; note disintegration of haustorial suspensor and absence of root cap. × 105. Figs. 102-107, maturation of coiled embryo. × 6. (*ps*, plumular scale; *pt*, remnants of pollen tube; *r*, radicular end; *s*, haustorial synergid; *st*, stem tip; *vs*, vascular strand).

divide so that in the first case there is no endosperm (Fig. 114) and in the second there is no embryo (Fig. 115). Sometimes even if the oospore and the primary endosperm nucleus both divide, the former does not proceed very far while the endosperm develops normally (Fig. 116). In the first case the ovule remains sterile and degenerates early. In the other two cases an exembryonate seed may be formed.

A very common cause (or accompaniment) of sterility is the excessive growth of the placenta after fertilization either from the side (Fig. 117) or from the base (Fig. 118) so that ovules get crushed and degenerate. A large number of normal-sized immature fruits, therefore, show only a spongy growth of the placenta with greatly shrivelled ovules.

The number of fertile seeds is very small and only two to three per cent are viable.

Discussion

The present study has revealed several special features some of which may be considered in detail.

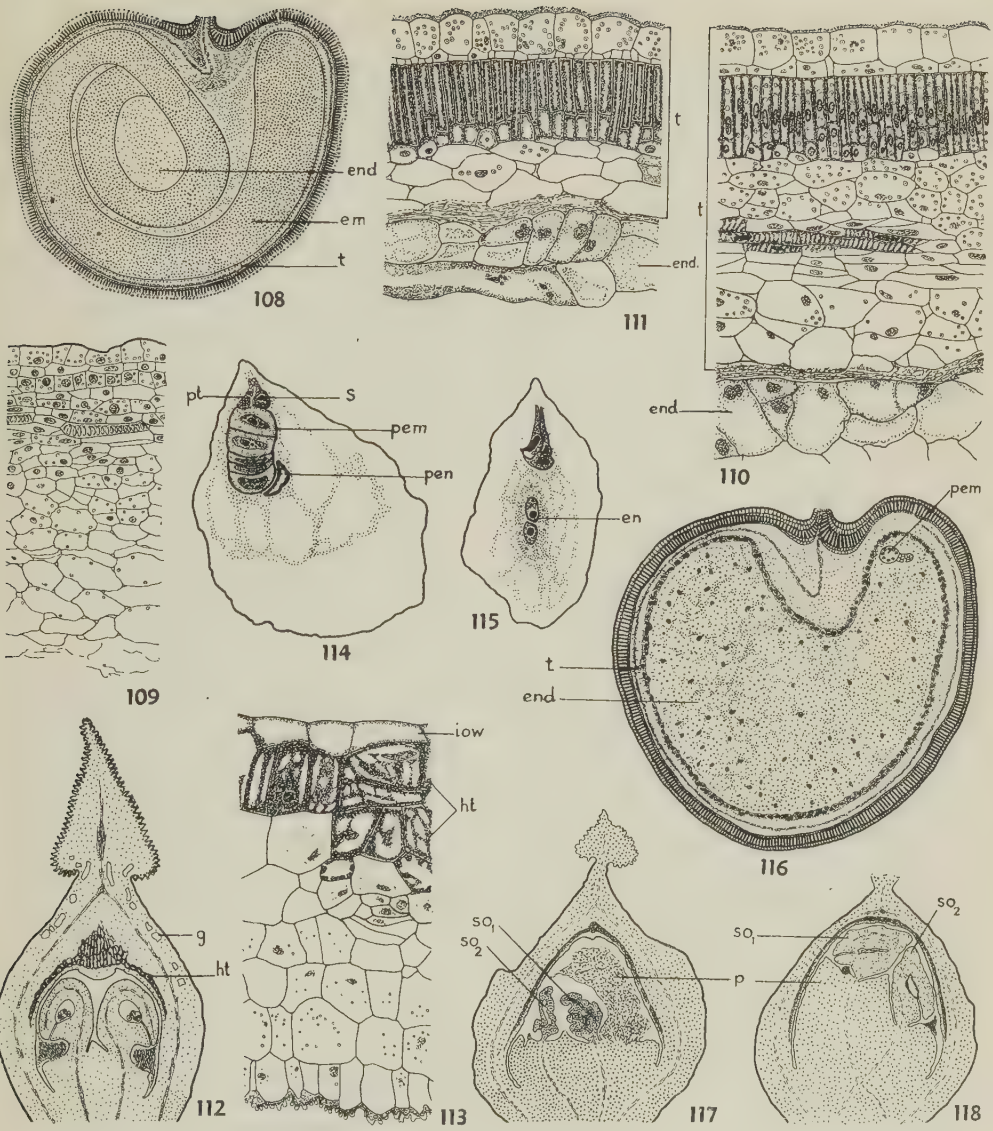
A three-celled condition of the mature pollen grain is common to all the species of *Cuscuta* studied so far (Fedortschuk, 1931; Smith, 1934; Finn, 1937; Tiagi, 1951). Fedortschuk reported that in *C. monogyna* the pollen grain is shed at the two-celled stage with the generative cell in prophase, its division taking place on the stigma in the pollen tube. Finn (1937) has corrected this observation and states that the mature pollen grains are three-celled before shedding. In *C. reflexa* the percentage of three-celled pollen grains is very small. It is likely that both two- and three-celled pollen grains are shed, and that in the former case the generative cell divides subsequently as in *C. monogyna*. Fedortschuk's detailed observations may, therefore, be correct and she may have overlooked three-celled pollen grains due to their smaller numbers. Finn has also pointed out that due to environmental influences sperm formation may be delayed and the division of the generative cell may be carried over to the pollen tube.

Multinucleate pollen grains have been reported in a number of plants particularly hybrids and may be usually sterile. In *Hyacinthus* and *Kniphofia*, Moffett (1932) considers that the multinucleate condition may be due to a genetic factor which shows itself only under certain environmental conditions of growth, i.e. due to a genetic developmental reaction. A similar factor may also affect the spindle mechanism of *Kniphofia* which accounts for the localized formation of giant pollen grains.

Heat treatment induced an embryo sac-like enlargement of the pollen grains in *Hyacinthus orientalis* and the nuclei increased to eight by a series of supernumerary mitoses (Stow[3], 1930). Naithani[3] (1937) has confirmed it in another variety of the above species and considers that this abnormal increase in size of the pollen grains is due to a temperature effect rather than to the liberation of "necro-hormones" from aborting pollen. In *Ornithogalum nutans* Geitler[3] (1941) observed, along with normal and degenerating pollen grains, others with eight or sixteen nuclei. It may be assumed that irregularities during meiosis, failure of wall formation in tetrad and supernumerary mitoses in the microspore or the pollen grain may be due to genetic or physiological and environmental factors.

Transformations of carpellary tissue into anther locule or stamens are rather rare. Chamberlain (1897) and Hagerup (1938) reported such an occurrence in *Salix*, Rao (1940) in *Dianthus* and Farooq (1952) in *Citrus*. Hagerup's observations deserve closer examination. Three types of transformations have been described. Part of the carpellary wall may develop a pollen sac as is the case in *Cuscuta reflexa* and probably in *Citrus*. Secondly, one or both the carpels may develop an anther at the apex with or without any trace of the style and stigma at the distal end. Thirdly, in some cases one or more ovules may be replaced individually by an anther. Hagerup concludes by saying that " the ovule and the stamen are equivalent organs " so that " the anther is homologous with the nucellus and the filament with the funicle ". That such teratological specimens, even though of

3. Quoted from Maheshwari (1949).



FIGS. 108-118. Fig. 108, l.s. mature seed showing coiled embryo and remnants of endosperm (diagrammatic). × 9. Figs. 109-111, t.s. testa showing consumption of inner parenchymatous layers by the endosperm. × 118. Fig. 112, l.s. ovary showing fibrous thickenings *ht* in hypodermal layers of inner ovary wall. × 17. Fig. 113, part of ovary wall enlarged to show details. × 118. Fig. 114, embryo sac showing five-celled proembryo and undivided primary endosperm nucleus. × 118. Fig. 115, egg apparatus degenerated but both the endosperm nuclei are quite healthy. × 118. Fig. 116, exembryonate seed with well-formed endosperm and a small slightly displaced proembryo. × 9. Figs. 117, 118, l.s. ovaries showing crushed ovules and an unusual spongy growth of the placenta. × 9. (*em*, embryo; *en*, endosperm nuclei; *end*, endosperm; *g*, gum cell; *ht*, hypodermal thickenings; *iow*, inner ovary wall; *p*, placenta; *pem*, proembryo; *pen*, primary endosperm nucleus; *pt*, pollen tube; *s*, haustorial synergid; *so*, sterile ovule; *t*, testa.)

regular occurrence, should have been made the basis of proposing homologies does not appear satisfactory to us. The morphology of the gynaecium is a controversial subject and we must await further information before attempting a satisfactory explanation.

Only a monosporic embryo sac of Polygonum type has been reported in the species of *Cuscuta* so far investigated excepting only *C. reflexa*. This led Finn (1937) and Maheshwari (1941) to doubt the observations of Johri and Nand (1934). However, the present work fully confirms Johri's earlier observations and the embryo sac is of the Allium type as originally stated. Such a variation is not common within the limits of the same genus but does occur occasionally. It is of interest to note that in different species of the genus *Euphorbia*, four types of embryo sac development — Polygonum, Allium, Peperomia and Fritillaria — are known (see Maheshwari & Johri, 1941). Similarly, all species of *Scilla* were so far considered to conform to Allium type (Maheshwari, 1950), but Govindappa and Sheriff (1951) have recently reported a Polygonum type in *S. indica*.

The development of the embryo is very characteristic. The suspensor of *C. reflexa* is comparable with the two types reported in *C. monogyna*, *C. epithymum*, *C. hyalina* and *C. planiflora* (Fedortschuk, 1931; Tiagi, 1951). To our knowledge similar observations have not been made in any other genus. Macpherson's (1921) account of the embryogeny of *C. gronovii* is very confusing and incomplete. She describes two types of embryos — spherical and elongated — with a suspensor of one or two cells or no suspensor at all.

Johansen (1950) includes the embryos of *C. monogyna* and *C. epithymum* (Fedortschuk, 1931) under the Caryophyllad type, Corydalis variation, on the assumption that the basal cell does not divide and the suspensor consists of vesicular cells. However, according to Fedortschuk, the embryogeny of both these species is quite different. In *C. monogyna* the basal cell remains undivided and a suspensor of four multinucleate vesicular cells is formed, part of the suspensor being derived from the terminal cell of the two-celled proembryo. In *C. epithymum*, also *C. hyalina* and *C. planiflora*, the basal cell divides to form a multicelled suspensor of uninucleate non-vesicular cells. Therefore, the emrbyo of these three species cannot be included under the Caryophyllad type but it may be considered under the Solanad type.

It is evident that Johansen's assignment of the embryos of *Cuscuta* is unsatisfactory. In *C. reflexa* the basal cell of the two-celled proembryo divides and the derivatives of the terminal cell also contribute to the suspensor. The latter consists of two to five multinucleate vesicular cells as well as a few uninucleate nonvesicular cells. It conforms to the Solanad type. Under this type only the Sherardia variation includes swollen haustorial suspensors but the embryo of *C. reflexa* is very different from that of *Sherardia arvensis* (Johansen, 1950) in having two types of suspensors, the absence of a histogenic differentiation in proembryo, presence of a coiled embryo without any trace of cotyledons and the absence of a root cap.

The behaviour of the basal and terminal cells of a two-celled proembryo is so variable that if sub-types (variations, according to Johansen) continued to be erected to include them, the problem will become far more confused than ever. In fact, our knowledge of the embryogeny of angiosperms is as yet very meagre and it may be possible to evolve a satisfactory classification only after a good deal more has been known.

Tiagi (1951) has compared the embryological features of *Cuscuta* with those of the Convolvulaceae. The parasitic habit of *Cuscuta*, presence of a corona, absence of a parietal cell in the nucellus, mono- or bisporic origin of the embryo sac, persistent and haustorial nature of one of the synergids, aggressive activity of the endosperm, a suspensor of coenocytic and vesicular cells or of uninucleate nonvesicular cells, lack of histogenic differentiation in the proembryo, a filiform spirally coiled embryo without differentiation into cotyledons and an endospermic seed are characters which warrant the separation of *Cuscuta* from the Convolvulaceae

into a separate family Cuscutaceae. We, therefore, agree with Wettstein (1935) who has already erected this family (see also Hooker, 1885; Rendle, 1925; Hutchinson, 1926; Fernald, 1950).

Summary

The pentamerous flower shows a corona of five fimbriate scales situated at the base of the corolla tube below the epipetalous stamens. The gynaecium is bi- or sometimes tricarpellary with an imperfectly partitioned two- or three-celled ovary. Each locule shows two ovules attached on a basal axile placenta.

Microsporogenesis proceeds in the usual way. The tapetum is glandular and its cells become two- to three-nucleate. The mature anther shows a large number of two-celled and a smaller percentage of three-celled pollen grains with four, five or six germinal furrows. A large number of pollen grains are sterile.

In rare cases polyspory and multinucleate pollen grains were observed. They may arise from failure of wall formation during meiosis or supernumerary divisions of the microspore or the pollen grain nucleus. One or more microspores often remain fused to form the compound pollen grains.

The unitegmic, tenuinucellate ovule is anatropous. The placenta proliferates at the base of each ovule to form a glandular obturator which comes in close proximity to the micropyle.

The development of the embryo sac conforms to the Allium type. Usually the antipodals degenerate before fertilization. One of the synergids becomes hypertrophied and persists for a long time. Some abnormal embryo sacs have been observed.

Double fertilization occurs. One fertilized embryo sac showed remnants of three pollen tubes and ten (or eleven) sperm cells lying in the synergids. Polyspermy may, therefore, occur in the pollen grain or the pollen tube and one of the synergids may be fertilized.

The oospore and the primary endosperm nucleus divide at about the same time but occasionally the latter may precede the former. The endosperm is free nuclear but later becomes cellular. The inner endosperm tissue gelatinizes forming a homogeneously staining mucilaginous matrix.

The oospore divides transversely into the basal and terminal cells. The suspensor is formed by the former and some derivatives of the terminal cell. It may be a haustorial structure consisting of two to five multinucleate vesicular cells or of several uninucleate ordinary cells. Intermediate types also occur. A short neck of two tiers of cells connects the suspensor with the proembryo.

By repeated transverse divisions the terminal cell produces a filamentous proembryo which undergoes irregular divisions to form a globular mass of cells. The mature embryo is spirally coiled and bears a few plumular scales but there is no differentiation of cotyledons.

Polyembryony occurs sometimes, the additional embryo being derived from one of the synergids.

A single seed matures in each ovary. It contains a scanty mucilaginous endosperm. The testa consists of remnants of the epidermis and the hypodermis and two layers of thick-walled lignified cells, the remaining layers of parenchymatous cells being consumed by the endosperm.

Even before fertilization lignified thickenings are formed in one or two hypodermal layers of the inner ovary wall. Later they break down due to an enlargement of the ovule. The dehiscence is circumscessile and the fruit wall comes off in the basal region.

Sterility of ovules is very common. It may be caused by lack of formation of the endosperm or the embryo in the fertilized embryo sac. In the former case the degeneration is very early while in the latter an ex-embryonate seed full of endosperm may be formed. Sterility may also be due to a spongy growth of the placenta which crushes the ovules.

Only two to three per cent of the seeds are viable.

It is a great pleasure to express our sincere gratitude to Prof. P. Maheshwari for his kind help and interest in the preparation of this work. The junior author is also obliged to Principal V. V. John of Government College, Ajmer, for facilities and encouragement.

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JOHN THEODORE BUCHHOLZ, 1888-1951

G. NEVILLE JONES AND OSWALD TIPPO
Department of Botany, University of Illinois, Urbana, Illinois, U.S.A.

The late Professor John Theodore Buchholz was one of the most distinguished botanists of his time. He was an outstanding authority on the morphology of plants, especially on the structure and evolution of gymnosperms. Between 1913 and 1951, he published nearly one hundred research papers on embryology of conifers, morphology and taxonomy of gymnosperms, and on various phases of genetics and cytology. The University of Illinois has lost an effective teacher and one of its most productive scholars.

Dr. Buchholz's contributions to science were recognized here and abroad. In 1941 he served as president of the Botanical Society of America. In 1942 he was vice-president of the botanical section of the American Association for the Advancement of Science. At the centennial celebration of the State University of Iowa in 1947, he was chosen as one of the most distinguished alumni of that university. At the International Botanical Congress at Stockholm in the summer of 1950 he served as vice-president of the section on plant morphology. He was elected Correspondent of the Museum of Natural History of Paris in 1950, in recognition of his outstanding studies of the botany of New Caledonia.

Dr. Buchholz's early life was spent in Nebraska, where he was born on July 14, 1888. He had the distinction of receiving two degrees in the same year (1909): Bachelor of Science from Iowa Wesleyan College, and Bachelor of Arts from the State University of Iowa. His graduate study was at the University of Chicago; his research was with Charles J. Chamberlain, authority on cycads and other gymnosperms, who had studied earlier with Strasburger at Bonn. Buchholz served as a fellow in botany at Chicago in 1916-1917, and received the degree of Doctor of Philosophy in 1917.

He was married to Olive Peterson on August 15, 1912. They had three children, Miriam, Christine, and Ruth.

Dr. Buchholz was instructor in biology at Arkansas State Normal School in Conway from 1909 to 1911, and head of the science department of that institution from 1911 to 1918. He was professor of biology at West Texas State Normal College at Canyon City, 1918-1919; professor and head of the Department of

JOHN THEODORE BUCHHOLZ.

Botany, University of Arkansas, 1919-1926, and professor of botany, University of Texas, 1926-1929. He came to the University of Illinois as professor of botany in 1929, and was head of the department from 1938 to 1942. During summers, 1921 to 1941, he was visiting investigator in the Department of Genetics, Carnegie Institution, Cold Spring Harbor, New York.

During the academic year of 1947-48, Dr. Buchholz had sabbatical leave in New Caledonia, where he and Mrs. Buchholz studied the flora, and made a large collection of botanical specimens for the herbarium of this university. Several research papers were published on the basis of these studies, during which he discovered fifteen new species of vascular plants. Nine of these were cone-bearing trees, which he subsequently described and named. Professor A. Guillaumin of the Natural History Museum in Paris, to whom Dr. Buchholz sent some of his collections, named one of the flowering plants *Baloghia buchholzii* (Euphorbiaceae).

Mr. and Mrs. Buchholz spent the summer of 1950 in Europe. At the Paris Museum he studied collections of New Caledonian plants, and continued his monographic work on conifers. He spent several weeks in England continuing research at the British Museum, the Royal Botanic Gardens at Kew, and in the herbarium of Cambridge University. They went on to Sweden to attend the meetings of the International Botanical Congress, where Professor Buchholz presented two invitation papers. He was the official delegate of the University of Illinois at this Congress.

Mrs. Buchholz was killed in an automobile accident on April 23, 1951, at a railroad crossing near Armington, Illinois. Her husband died after a short illness, six weeks later, on July 1, 1951, at Urbana, two weeks short of his 63rd birthday.

Buchholz was author of the article on gymnosperms in the *Encyclopaedia Britannica*, 1946, and one of the most distinguished authorities on this group of plants. He did pioneer work on the study of chromosome structure with the electron microscope. For twenty years he studied the genetics of *Datura*. His name will be always associated with the big-tree of the Sierra Nevada, which after years of thorough embryological, morphological, and taxonomic study, he renamed *Sequoiadendron*, showing by abundant evidence its generic distinctness from the coast redwood.

His life was one of distinguished effectiveness in fields requiring difficult study and patient endeavour. He was a true investigator, always faithful to his ideals of professional action and human relations. He manifested a warm spirit of friendliness, companionship, and helpfulness. The university has lost a scholar of wide interest, an able and enthusiastic investigator, and a staunch friend.

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1. Acknowledgement is made to Mr. Cheng-Lee Lee, one of Dr. Buchholz's students, for assembling the data for the preparation of the bibliography.

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REVIEWS

ARBER, AGNES. 1950. "The Natural Philosophy of Plant Form." Pp. 247; text-figures 46 (each containing several separate drawings). Cambridge University Press. 25*s*.

Dr. Agnes Arber's contribution to plant morphology is perhaps the most magnificent in the present century. We have had numerous, very valuable and thought-provoking publications from her, but the present one, which embodies the results of thinking, analysis and synthesis for about half a century, is most welcome.

The scope of the book is best described by the author when she writes: "In the present study I have tried to express certain general ideas which have gradually disengaged themselves in my mind, in the course of a lifetime's concern with the morphology of flowering plants, both as it is understood today, and in its historical development from the time of Aristotle onwards." Herein she has admirably discussed in a lucid and graceful language, which few scientific writers can rival, "the relations of parts in the flowering plants in the light of those more universal and more stringent, modes of thought, which are characteristic of philosophy rather than of biology".

Several reviews of the book have already appeared but it deserves as wide a publicity as possible and can well bear many more comments.

Professor Sir Arthur Tansley has recently published a detailed review in the *New Phytologist* in which he disagrees with Dr. Arber on certain important points. The present reviewer has no intention of getting in between these two eminent British botanists of the present century, but he submits, though not without some hesitation, that Sir Arthur Tansley's comments betray lack of proper appreciation of Dr. Arber's point of view.

Dr. Arber's earlier works, particularly those dealing with the interpretation of 'Monocotyledons', 'root', 'shoot', 'flower' and 'leaf', help us in following the development of her thoughts as discussed in the present treatise which comprises 11 chapters, a detailed bibliography of about 400 titles with page references to the text, and a detailed subject index.

The first chapter is devoted to a discussion of the meaning and content of plant morphology. By 'morphology' she means the study of *form* in the widest sense. She contends that it is "the business of morphology to connect into one coherent whole all that may be held to belong to the intrinsic nature of a living being". *Form*, among plants, according to her, may be held to include something corresponding to behaviour in the animal world. She deprecates the modern tendency of equating 'morphology' with 'external morphology'.

Sir Arthur Tansley has taken exception to Dr. Arber's usage of the term 'form' in such a wide sense. According to him "the customary meaning of the word 'form' is too useful to be superseded in current usage". He, therefore, suggests that in the title of the book the word 'form' should be replaced by 'plant organism'.

In the next four chapters Dr. Arber gives a historical sketch of the development of plant morphology from Aristotle to pre-Darwinian times. Herein while one is delighted to read a well-documented account of the important contributions of Theophrastus, Magnus, Caesalpino, Jung, Malpighi, Grew, Goethe and de Candolle, one misses somewhat any reference to the ingenious, though ill-fated, theory of prolepsis of Linnaeus.

Then she traces the history of the 'organization type' concept and discusses in some detail the *Urpflanze* of Goethe and the influence of Darwinianism on this. Following Goethe she considers this as a concept from which the concepts of existing plant forms could be derived mentally. According to her it carries

" no phylogenetic implications ", and if any relations are recognized between two ' forms ', they are " logical " rather than " temporal ". Morphological series are, therefore, considered as " merely mental constructs with no validity in time ". This is one way of pursuing ' morphology ', though more difficult since it involves so much of mental picturing. The other which evolved with Darwinianism forced ' morphology ', so to say, into the framework of evolutionary biology. " To many workers at that time the diversion of biology into historical channels was a welcome relief, since it transformed theoretical botany into something material, amenable to picture-thinking and not demanding difficult mental activity of a metaphysical kind." Dr. Arber deprecates rather strongly this degradation of morphology to play a second fiddle to evolutionary biology. She has asserted elsewhere that " morphological and phylogenetic concepts belong to different categories and only confusion can come of the attempt to reduce these categories to one ".

To those morphologists who have ever dabbled with the problem of origin of angiosperms such an attitude " in so able a twentieth century morphologist " may not appear to be quite " surprising ". The disappointment which they have had to face in trying to discover the " common ancestor " has been so disastrous that it has almost shaken their faith in the doctrine of continuity. The sense of frustration which thus overtook them has awakened them to the importance of parallelism in evolution. Dr. Arber is among the earliest students in this comparatively new field (*see* her ' Monocotyledons ', 1925). Sir Arthur Tansley, perhaps little troubled with the trials and tribulations which these morphologists had to face, has not fully appreciated the swing in Dr. Arber's thought. He still seems to think of evolution in terms of a ' phylogenetic tree '. This is apparent from his assertion: " If we want to explore the problem of the foliage leaf at large, we cannot exclude the Pteridophytes, the microphyllous forms as well as the ferns and we must go further down still and consider the bryophytes and the adumbrations of leaf formation met with in the algae. " Dr. Arber has indeed shown very ingeniously how the problem of angiosperm leaf can be tackled without reference to any other group. This is undoubtedly her most remarkable contribution and we have got to recognize this.

The next three chapters are devoted to a consideration of leaf morphology and some other morphological problems related to it. She accepts Casimir de Candolle's idea of a leaf as " *a partial-shoot, arising laterally from a parent whole-shoot* ", and cites much evidence for this from her own work. This is indeed the main theme of the book. Her application of the same concept to the root, however, does not appear to be so convincing. She also goes on to offer interesting explanations for the morphology of axillary buds, ovuliferous scales, placenta, and ovule in the light of the partial shoot concept. It is indeed gratifying to see her synthesizing so admirably the apparently diverging views on the nature of these organs. However, while concluding these most fascinating chapters of the book she frankly admits the tentative nature of her suggestions. She writes: " That the partial-shoot theory, with its corollaries, is open to criticism in many directions is, however, obvious; the utmost that can be hoped is that it will be a temporary expedient for clarifying thought, and that it will serve as a step towards some future picture of plant construction which will achieve a higher degree of adequacy."

The present reviewer sees little difference in the partial-shoot theory of Dr. Arber and the telome theory of Professor Zimmermann. They are just two approaches to the same goal; one is ontogenetic, the other is phylogenetic. This is implied in Dr. Arber's own statement concerning the essential features of the telome theory: " If those views (about the leaves being primarily radial in structure and branched in all directions) were expressed in morphological rather than phylogenetic terms, they would in no way conflict with the partial shoot theory of leaf." This should clearly bring home to the reader the precise difference between

the outlook of Dr. Arber and that of her critic, Sir Arthur Tansley.

On page 108 a brief reference is also made to the leaf of monocotyledons. The old interpretation of its being a ' petiolar-phyllode ' is modified and it is now interpreted as " *a fixation of the whole phyllome at its pre-lamillar stage* ".

In chapter 9 Dr. Arber gives numerous examples of repetitive branching both in leaf and shoot, and draws pointed attention to the close parallelism between the two. She also describes here briefly Professor Troll's concept of *Gestalt* type and ultimately expresses the hope that this " may perhaps be absorbed into that (concept) of parallelism ".

The last two chapters are apparently metaphysical rather than botanical in their content and here it is demonstrated how this branch of natural science (botany) " reaches its fullest reality in the region of natural philosophy where it converges on metaphysics . . . " In a discussion of " the mechanism of plant morphology " she takes exception to the use of the common phrase, ' causal factors ', and suggests a more appropriate expression, ' conditioning factors '. In the treatment of teleology in the last chapter one misses any reference to the work of the late Professor Goebel.

The book is indeed an outstanding contribution from an eminent morphologist of long standing and vast experience. Some of the views dealt with have already been discussed in earlier communications, others have been put forward for the first time here. The main thesis dealt with in the book is the partial-shoot theory of leaf. It is very well documented and, in the light of this, interesting explanations have been offered of some of the other outstanding problems of plant morphology. The most remarkable feature of this theory and its corollaries is that they provide us a means of fusing into " inclusive " forms certain pairs of opposing views (as for instance axial *versus* foliar interpretations of axillary bud, ovuliferous scale, placenta, ovule, etc.) which have hitherto been regarded as mutually " exclusive ".

One may not agree, at the moment, with all what Dr. Arber says, but there is little doubt that the book provides a powerful stimulant to thought and as such deserves careful consideration. We have every reason to be grateful to Dr. Agnes Arber for this masterly work.

V. Puri

YOUNGKEN, H. W. 1951. " Pharmaceutical Botany." 7th Ed. The Blakiston Company, Philadelphia & Toronto. Pp. 752.

Approximately one half of the book deals with the morphology, anatomy and physiology of plants and is not essentially different from the treatment followed in many other text-books. One chapter deals with " Plant Environment " and one with " Genetics and Evolution ". The second half deals with a systematic study of the plant kingdom with special reference to the plants used in medicine. There are two appendices, one on the use of the microscope and the other on histological technique. In the end there is a useful glossary, a classified list of reference works and an index. A good many of the illustrations are borrowed; there is a long list of acknowledgements just after the preface, but in many cases the acknowledgement is made in the text. The latter is perhaps the more satisfactory method because it enables the reader to know immediately the source of the illustration instead of having to hunt behind in the preface and waste several minutes in the process.

The illustrations are not all of the same merit. To quote only one instance, Fig. 397A of the pollen grain of *Pinus* shows only one prothallial cell whereas there should have been two or at least the remains of two.

Although the get-up and presentation of material are generally satisfactory, the author sometimes uses a terminology which is not in accordance with modern thought. Thus, the ovuliferous scale of *Pinus* is considered equivalent to a megasporophyll, the ovule to a megasorus and the nucellus to a megasporangium. In *Ephedra* the author speaks of " fruits " although it is clear that in a true sense fruits do not occur in any gymnosperm. The Latin names of many plants need to

be corrected. Thus, *Eugenia caryophyllata* should probably be changed to *Syzygium aromaticum*, *Taraktogenos kurzii* to *Hydnocarpus kurzii*, and *Cochlospermum gossypium* to *C. religiosum*. It is hoped that the author will consider these points when bringing out the eighth edition of this popular text.

P. MAHESHWARI

DOUGLAS, J. S. 1951. "Hydroponics—The Bengal System." Oxford University Press, Bombay. Pp. 147. Rs. 6.

FOR the last few years "hydroponics" or soil-less culture of plants has been very much in the forefront and Mr. Douglas has rendered a distinct service in writing this popular and non-technical text supplying not only the historical background to this subject but also giving his own experiences in this line on the basis of experiments carried out in Bengal. The instructions which he gives are clear and concise and the illustrations are attractive. Although further research is necessary to perfect the soil-less method, the author believes that adequate success has already been achieved and is confident that "the Bengal system of hydroponics has entered the world of practical horticulture". In chapter VII he lists twenty-nine points of superiority of the soil-less method over the ordinary method and concludes in chapter X: "We may all confidently look forward to that not far distant day when there will be a hydroponicum in every home, banishing want, bringing economic independence, and ensuring that children of the future may grow up amid healthy surroundings with clean, fresh food to eat."

The reviewer is much interested in the science of hydroponics and considers that it has an undoubted value under emergency conditions as was proved during the war when Americans set up huge hydroponic systems in places in the Pacific, but whether it will be equally profitable under peace conditions and in places where reasonably fertile soil is available is still to be seen. The figures given by Mr. Douglas are not convincing for he compares the produce obtained by unskilled workers on poorly irrigated and imperfectly manured soil with that obtained by experts using all the available information regarding the mineral requirements of crops.

P. MAHESHWARI

BENSON, L. 1950. "The cacti of Arizona." University of Arizona Press, Tucson. Pp. 134. $ 4.00.

PROFESSOR LYMAN BENSON has long been interested in the cacti which are not far away from the place of his professional activities. In this small volume he has given a very attractive and usable account of the cacti of the south-west part of the U.S.A. There are good keys and distribution maps, and the text is amply illustrated with nice photographs some of which are in full colour.

The first 13 pages deal with the morphology, problems of classification and geographic distribution of cacti. The following 95 pages or so deal with species belonging to 5 genera: *Opuntia*, *Cereus*, *Echinocereus*, *Echinocactus* and *Mammillaria*. The last few pages give some useful hints on the methods of cultivating cacti.

In the preface the author refers to the prevailing impression about the difficulty of making herbarium specimens of cacti. Many amateurs and botanists would have appreciated some suggestions as to how this difficulty can be overcome and even the massive succulent parts of these plants made to fit the herbarium sheet.

The value of the book is slightly impaired by the lack of an index.

P. MAHESHWARI

FOSTER, A. S. 1950. "Practical Plant Anatomy." D. Van Nostrand Company Inc., Toronto, New York and London. 2nd Ed. Pp. 228.

THE results of recent studies on anatomy are recorded in such a large number of journals that it is becoming increasingly difficult for a student to make himself familiar with the advance of knowledge. Prof. Foster's book, therefore, is both timely and welcome. Written with a view "to provide for the student a means of articulating the practical study of laboratory material with the best of modern theory and interpretation", it presents a clear and concise survey of the more

important aspects of anatomy. The language is so simple that even an elementary student should have little trouble with it. References to literature in the text as well as at the end of each chapter provide sources of additional information.

The first three chapters deal with the Protoplast, Cell-wall and Meristems. Chapter IV deals with the classification of the cell types, tissues and tissue systems. The remaining eleven chapters, V-XV, deal with the Epidermis, Parenchyma, Collenchyma, Sclerenchyma (sclereides and fibres), Tracheids and Vessel elements, Laticiferous tubes, Stem, Leaf and Root. In the end there is a very useful Appendix giving methods of microtechnique for anatomical studies.

Each chapter deals with the structure of a cell type or tissue and describes its functions in a very concise and intelligible manner. Hints on the material for study and suggested drawings and notes at the end of each exercise are very valuable and reduce the unnecessary waste of time in trial and error by a beginner.

The book is very attractively produced and the only suggestions which the reviewer has to offer are that it should be illustrated and also incorporate some information on the study of the secondary xylem and phloem.

B. M. JOHRI

STOVER, E. L. 1951. "An Introduction to the Anatomy of Seed Plants." D. C. Heath & Company, Boston. Pp. 274. 21*s*.

THIS is a welcome addition to our textbooks on plant anatomy, its aim being to give the reader a dynamic sequence of the growth and development of the root, stem and leaves of seed plants from the fertilized egg onward. The anatomy of the flower, fruit and seed, and anatomical specializations from the viewpoint of an evolutionary sequence of plant groups have not been included; and to that extent the text is incomplete.

There are fourteen chapters, each with a short bibliography. The first chapter deals briefly with the embryo of gymnosperms and angiosperms without any account, however, of the development and differentiation of the epicotyledonary stem tip. In the chapter on "Seedling" the anatomy of the root-stem transition region has not been dealt with. An inclusion of some diagrams to explain secondary growth and formation of lateral roots would have improved the third chapter on "Root and Root Systems". Since beginners must first have an aquaintance with cells and tissues before having an introduction to the structure of the organs, it would perhaps have been better to place the fourth chapter on "Cells and Tissues" just before or after the chapter on "Embryo". Thickenings of the cell-wall have not been elaborated or properly illustrated. The fifth chapter on "Buds and the Development of Leaves" deals with the morphology of buds, leaf origin and differentiation and the structure of the mature leaf, but the different types of stomata have not been described either here or at any other place in the book. Chapters VI, VII and VIII give a comparative account of the mesomorphic and xeromorphic leaves of gymnosperms, and the mesomorphic, hydromorphic and xeromorphic leaves of angiosperms. Chapter IX deals with the external morphology of herbaceous stems, especially rhizomes, bulbs, corms and tubers, and of woody stems; also the gross internal structure of herbaceous and woody plants. It could perhaps have been improved by adding an account of the internal structure of underground stems. Chapter X describes the origin and development of the tissues in stems. The chapter on vegetative propagation leans more towards external morphology than anatomy but gives a brief account of cuttings from roots, stems and leaves, of coppicing, grafting, and 'foliar embryos'. Vegetative propagation from callus and from cells of the epidermis also receives attention. "Wood" forms the subject-matter of chapters XII and XIII. A key for the identification of important American woods has been given in the last chapter.

The book under review is a very good introduction to anatomy for a one-semester course. The inclusion of information on vegetative propagation, wood, and the identification of woods is most welcome.

G. C. MITRA

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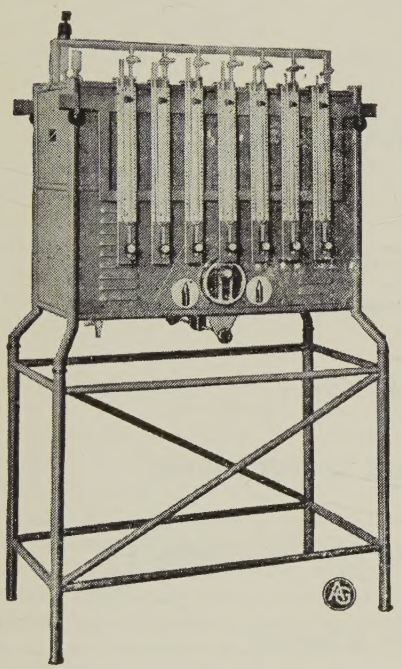

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